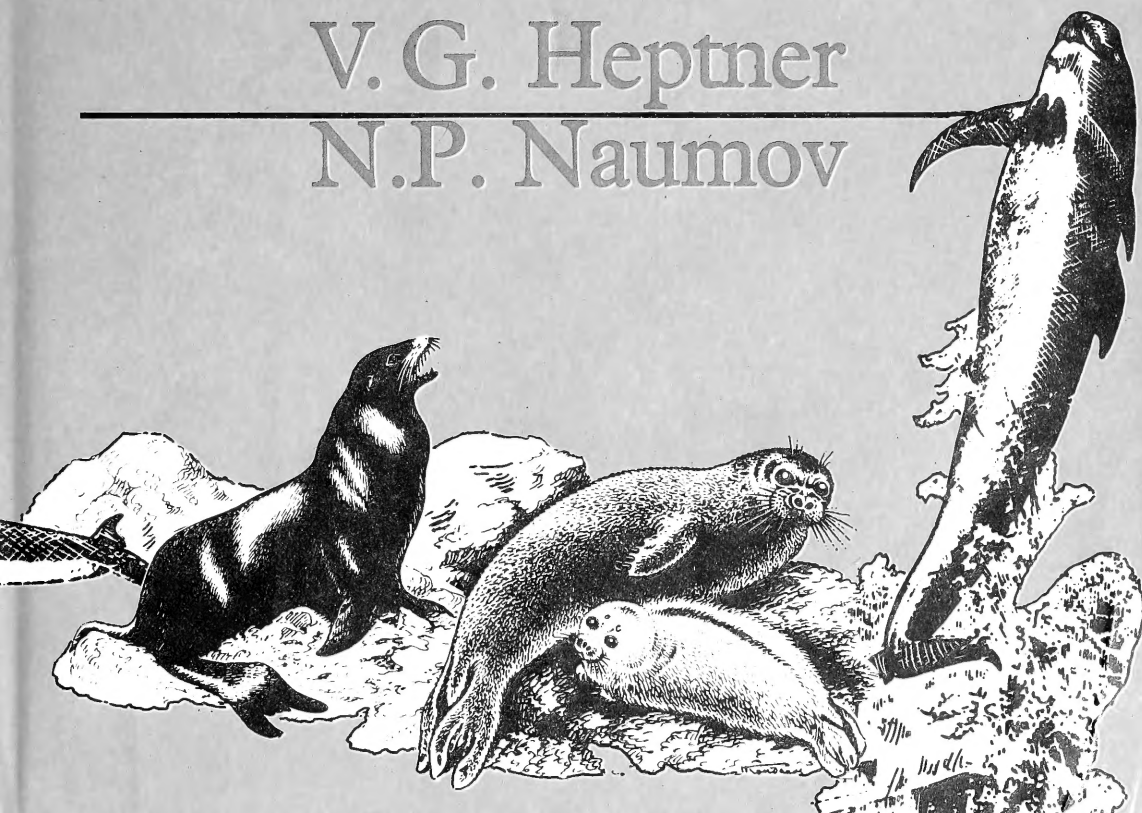


Mammals of the Soviet Union

VOLUME II Part 3

V. G. Heptner
N. P. Naumov



This is the fourth book of *Mammals of the Soviet Union*, representing the third part of the second volume; it is devoted to descriptions of the orders of Soviet aquatic mammals — pinnipeds (Pinnipedia) and, in part, cetaceans (Cetacea), toothed whales (Odontoceti). In the sequence of descriptions from the “higher” to the “lower” orders adopted in this series, pinnipeds should have preceded carnivores, i.e., should have appeared in the second book. The grouping of the orders at a higher level is given after G.G. Simpson (1945). The sequence of genera and species within the orders has been retained as before, i.e., from the less specialized to the more specialized.

The order of pinnipeds or seals (Pinnipedia) is described in this volume. The cohort of ungulates and carnivores represented in Soviet fauna by orders of artiodactyls, and perissodactyls, sirenians, carnivores, and pinnipeds thus comes to an end and the cohort of whales (Mutica) commences. The toothed whales are described in this volume.

While it has not always been possible to maintain a totally uniform description of the genera and species as in the volumes already published, in spite of every effort to do so, the sequence has been adhered to, with some exceptions, in the case of Pinnipedia. But, it was impossible to use sane format in describing the toothed whales (Odontoceti). Only a brief morphological description has been given for many species, which is more or less adequate for identifying the species. General information on their distribution and fragmentary biological data are also given. In some cases the total absence of such information is indicated.

Robert S Hoffman
August 1996

Mammals of the Soviet Union

Volume II, Part 3

MAMMALS OF THE SOVIET UNION

In Three Volumes

Edited by
Late V.G. Heptner and N.P. Naumov

Vysshaya Shkola Publishers
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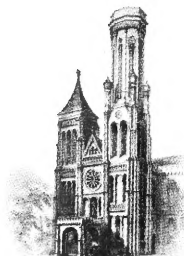
VOLUME II, Part 3

PINNIPEDS AND TOOTHED WHALES
Pinnipedia and Odontoceti

Late V.G. Heptner, K.K. Chapskii, V.A. Arsen'ev
and V.E. Sokolov

Edited by
Late V.G. Heptner

Scientific Editor
JAMES G. MEAD



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Most of the reference materials utilized were published before the end of the 1960s, although a few books and articles from more recent years have been useful. References are cited in the text by the author's name without initials and with the year of publication. Initials are used only when the surnames are identical. References to authors of unpublished private communications are also made in parentheses but with initials and without the year. The bibliography at the end of the book covers only the references cited (although many more were reviewed),

excluding those listed under synonyms. As in the previous publications, the authors have included, quite naturally, their own unpublished material in the text.

The preceding volumes of *Mammals of the Soviet Union* have been warmly received within and outside the USSR. The first three books in the series were translated into German. The authors hope that this volume, too, will be as warmly received although they are aware of its several shortcomings. An explanation for this, although not a justification, is the complicated nature of the material, especially that of whales. Save for some individual species, the museums in the USSR contain practically no collections of this group.

V.G. Heptner



FOREWORD TO THE ENGLISH EDITION

The Smithsonian Institution Libraries, in cooperation with the National Science Foundation, has sponsored the translation into English of this and hundreds of other scientific and scholarly studies since 1960. The program, funded with Special Foreign Currency under the provisions of Public Law 480, represents an investment in the dissemination of knowledge to which the Smithsonian Institution is dedicated.

One of the values of this translated volume is to give English readers an insight into another philosophical system that devoted nearly a century to the studies of marine mammals. This work is important because it has an abundance of data that were taken from commercial harvest, particularly from small cetaceans, that have been generally unavailable to the English-speaking community. A monograph of this magnitude, with such an extensive bibliography, serves as an excellent entrée into the Russian literature.

This volume is the last to be published under the general editorship of V.G. Heptner and N.P. Naumov; Volume II, part 3, Pinnipeds and Toothed-whales appeared in 1976, the year after Professor Heptner's death. Only one more volume of the original series remains to be published in an English edition, Volume II, Part 1, Sea Cows and Carnivores (Dogs, Bears, and Mustelids), but editing of the English language manuscript is about 60 percent complete, and it is the intention of the Smithsonian Libraries Translation Program to publish the volume as soon as possible.

After a lapse of two decades, the series has been revived with the sponsorship of the Russian Academy of Sciences' Institute of Evolutionary Animal Morphology and Ecology in Moscow, with a new series title reflecting recent political changes—*Mammals of Russia and Bordering Regions*. The first volume in this new series is, as had been anticipated, *Usatye Kity* [Baleen Whales], by V.E. Sokolov and V.A. Arsen'ev (1994, Nauka, Moscow, 208 pp.). A second volume on *Zaitseobraznye* [Lagomorphs] is in production. It is hoped (but by no means certain) that English editions of the revived series can be made available.

English readers interested in Dr. Heptner's contributions as a mammalogist should refer to the Foreword to the English Edition of Volume I. Conventions used in rendering geographic names, first stated there, are reprinted here for the convenience of the reader. Geographic names are generally transliterated directly, but a few exceptions were permitted (e.g. Moscow instead of Moskva, translation rather than transliteration of certain modifiers of place names, such as Northern, rather than Severnaya Dvina). Soviet administrative units are numerous, and the following equivalents were employed in translation: Krai, territory; oblast', district; raion, region; guberniya (archaic), province. Also, in the original Russian text, rivers, mountain ranges, and cities are often not explicitly identified, the Soviet reader being presumed sufficiently familiar with the geography of the country to be able to understand from the context of the sentence what sort of place is referred to. Complicating the matter is the lack of articles as parts of speech in Russian. To assist the English reader, the following conventions have been adopted: if a river is referred to, an article precedes it; if a mountain range is referred to, it is translated as a plural; if a city is referred to, it is singular, and lacks the article. Examples are: the Ural (river); the Urals (mountains); Ural'sk (city). Geographic place names are also inflected in Russian, and these have been simplified by omitting transliteration of the inflected ending. For example, the Russian phrase *v Yaroslavskoi i Kostromskoi oblastiakh* is translated "in the Yaroslavl' and Kostroma districts." In cases where the nominative form of the place name has an -sk ending this is, however, transliterated (e.g., Omsk); when a Russian "soft sign" is employed in a place name, this is transliterated as an apostrophe (e.g., Khar'kov).

As in any translation, particularly from one orthography into another, there arise problems of standardization of names. For geographic names the *National Geographic Atlas of the World*, 4th edition, 1975 was used for this volume (principally the map on pages 122-123). Some of the geographic terms like gulf, bay, inlet, strait [*zaliv, bukhta, guba, proliv*] are used in slightly different contexts in the original Russian text. Because of the large number of place names in this volume, it was not possible to verify all of them, and some inconsistencies are likely to occur. We would appreciate it if readers would bring any errors they may notice to our attention.

The usage of the common terms "dolphin" and "porpoises" varies geographically. In North America these terms are used interchangeably in reference to members of the family Delphinidae (sensu Simpson 1945) but only the term "porpoise" is used to refer to members of the family Phocoenidae (sensu Simpson 1945). In most other English speaking

countries, including England, the term “dolphin” is restricted to reference to the family Delphinidae. In Russian, the term “del’fin” (dolphin) is used to refer to all of the members of the family Delphinidae and the term “morskaya svinya” (sea pig), which is equivalent to the meaning of the Latin roots of “porpoise” (porcus = pig + piscis = fish) is used to refer to the members of the family Phocoenidae. We have therefore chosen to use the more restrictive English usage in this volume.

A few of the vernacular names, those where the Russian name was vastly different from the generally accepted English name, have been changed, but translations of Russian vernacular names were employed where there was not a generally accepted English term (e.g. the vernacular name of the genus *Lagenorhynchus*). There is no English vernacular name for members of the genus *Mesoplodon*; Mead prefers to translate the Russian term “remnezubov” (sword-toothed) as *Mesoplodon*, rather than a literal translation. In addition, recent systematic studies have shown that the appropriate scientific name for the Malay dolphin (*Stenella dubia*) is *Stenella attenuata* (= Pan-tropical spotted dolphin) and the English common name of the Bridled dolphin (*Stenella frontalis*) is Atlantic spotted dolphin.

Some terms placed in brackets [] indicate that they are additions of the scientific editor and are not found in the Russian text. In statistical references, \bar{x} replaces M (mean), a much more accepted symbol for “mean” in English works.

One further point of confusion not apparent when Volume I was translated also requires clarification; that is the English transliteration of the senior author’s surname. This begins with the fourth letter of the Cyrillic alphabet, which usually has a “G” sound in Russian. However, the surname was originally German, and in the original German began with the letter “H” of the Latin alphabet. Since Cyrillic has no equivalent of “H” this is usually transliterated into “G” in Russian. However, Hoffmann, from conversations learned that Dr. Heptner preferred to use the original Germanic form of his surname rather than the transliterated version, which is rendered as Geptner. The rules of transliteration employed by the Library of Congress do not permit such flexibility, and the attentive reader may notice that Library of Congress cataloging employs the latter.

The Series Scientific Editor expresses particular thanks to the editor of this volume, Dr. James G. Mead, Curator of Marine Mammal Project, Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution. Dr. Mead’s broad knowledge of all aspects of marine mammal biology was critical to the quality of this English edition, and I am grateful to him for the considerable time he has

devoted to ensuring the accuracy of the volume. Thanks are also due to P.M. Rao and Dr. V.S. Kothekar, Translator and General Editor respectively of Amerind Publishing Company, New Delhi, India, for producing the original translation under the provisions of U.S. Public Law 480. Credit also must be given to the general editorial staff of Amerind Publishing Co., who confirmed all of the technical names of the prey species and parasites, checked the bibliographic references and translated many obscure Russian scientific terms.

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FOREWORD

This is the fourth book of *Mammals of the Soviet Union*, representing the third part of the second volume; it is devoted to descriptions of the orders of our [Soviet] aquatic mammals—pinnipeds (Pinnipedia) and, in part, cetaceans (Cetacea), toothed whales (Odontoceti). In the sequence of descriptions from the “higher” to the “lower” orders adopted in this series, pinnipeds should have preceded carnivores, i.e., should have appeared in the second book. The microsystem of the class is given below to elucidate the natural sequence and the relationships between orders. This is a simple and presently more widely used system, but pinnipeds have been assigned the status of an order and not a suborder as commonly accepted. The grouping of the orders at a higher level is given after G.G. Simpson (1945). The sequence of genera and species within the orders has been retained as before, i.e., from the less specialized to the more specialized.

The order of pinnipeds or seals (Pinnipedia) is described in this volume. The cohort of ungulates and carnivores represented in our [Soviet] fauna by orders of artiodactyls and perissodactyls, sirenians, carnivores, and pinnipeds thus comes to an end and the cohort of whales (Mutica) commences. The toothed whales are described in this volume and the baleen whales will be taken up in the next volume.

While it has not always been possible to maintain a totally uniform description of the genera and species as in the volumes already published, in spite of every effort to do so, the sequence has been adhered to, with some exceptions, in the case of Pinnipedia. But, it was impossible to use the same format in describing the toothed whales (Odontoceti). Firstly, the biology of nearly all the species, except the Black Sea species, is not adequately known even in respect of principal features, and information on their distribution is more scant. Only a brief morphological description has been given for many species, which is more or less adequate for identifying the species. General information on their distribution and fragmentary biological data are also given. In some cases the total absence of such information is indicated. Secondly, the faunal composition of the Soviet Pacific waters is not yet clear. While the presence

of some species already reported calls for confirmation, several species known from the coastal waters of Japan have not been reported in our waters. Some of them are found on the American coasts at the same latitudes. Their presence in our waters even as "stray" finds is highly probable; such probable species have been indicated, included in the keys, and briefly described. In this regard the present volume has achieved its aim, not only to describe the known species, but also to draw attention to the unknown. Such species total 14 while the number of relatively well-known species in the Soviet Pacific waters is quite large. While using the keys and morphological characteristics of the Pacific dolphins, reported here for the first time from our waters, their identification should be checked with the available literature and museum specimens. Interesting finds could be anticipated in the Soviet Far East and each case of a "stray" report or capture should be studied carefully. The probable species and genera have been given without numbers and in small print.

The ranges of distribution of every species have been compiled on the same principle as in the preceding books. However, in view of the specificity of the biology of marine species (long migrations), in many cases they are given in a more general form. The range extending beyond our waters is mainly based on the works of Van den Brink (1958), Schaffer (1958), Hall and Kelson (1959), King (1964), Hershkovitz (1966), Siivonen (1967), and some others, mostly of Japanese authors. The latter have been cited in the text. The entire synonymy has been selected on the principles adopted earlier (see Foreword to Vol. I and Vol. II, parts 1 and 2). In view of the scant indigenous literature on whales, their synonymy is given very briefly. A more complete list of the synonyms of the species of this order can be found in the monograph by Hershkovitz (1966).

The total number of species constituting this class is roughly 3,500, of which about 300 are represented in our fauna (Heptner, 1956). Almost all the illustrations in this book are original with the exception of those of the toothed whales taken from Hall and Kelson (1959). The original drawings are by the well-known Russian artist N.N. Kondakov who, apart from being a talented artist, is an experienced zoologist. Other sources of the drawings have been acknowledged at the appropriate place.

The contribution of each author to this volume is as follows. K.K. Chapskii wrote the general outline of the order Pinnipedia and the family of seals (Phocidae), gave the keys to the families of the order and species of the family of seals, and wrote the text on all the species of this family except for the Baikal seal, *Phoca sibirica*, and the ribbon seal, *Phoca fasciata*. V.A. Arsen'ev wrote the characteristics of the walrus (Odobenidae) and the eared seals (Otariidae), and the entire description

of walruses, sea lions, fur seals, and the ribbon and Baikal seals. He also wrote the sections on the distribution, biology, and economic importance of all the species of toothed whales (Odontoceti), the characteristics of the suborder of baleen whales (Mysticeti), and the outlines of all the species of this suborder which, as mentioned above, will be included in the next volume. V.E. Sokolov wrote the general outline of the order of cetaceans, suborder of toothed whales, and the description of all the genera of this suborder and the morphological characteristics of its species. V.G. Heptner wrote the introduction to the book, keys to the species of eared seals (Otariidae), and an outline of the genera and species of sea lions (*Zalophus californianus*). Moreover, he worked out the entire synonymy and participated in the compilation of notes on the distribution of many species. As in the preceding books, the individual authorship has been shown by initials within parentheses at the end of the pertinent section. The overall format, the system adopted, selection and sequence of the species, their scope, and the numbers and scope of the subspecies have been confirmed by V.G. Heptner.



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CLASSIFICATION OF CLASS MAMMALIA

In this publication the old and widely used system of the major units of the class, i.e., orders, has been adopted. There is only one feature in it which cannot be considered universal: pinnipeds are considered an independent order and not a suborder of carnivores (Carnivora). However, this approach, too, has many supporters. In the system of present-day mammals, these two groups are separated naturally and fully, no less than other orders. However, the close genetic relationship between pinnipeds and land carnivores is striking and beyond doubt.

The system of orders adopted here is well founded, being based on the morphology of present-day forms by M. Weber (1928) and of fossil forms by G.G. Simpson (1945). The grouping of orders into taxa of a much higher rank and the sequence of orders is after Simpson.

A tendency toward an extreme division of the orders has recently developed. Thus it has been proposed that the order of marsupials (Marsupialia) be divided into three (Polyprotodontoidea, Caenolestoidea, and Diprotodontoidea) and even five (Didelphia, Dasyuria, Peramelia, Caenolestia, and Phalangeria); insectivores into four (Insectivora proper, Zalambdodonta, Macroscelidea, and Tupaioidea); cetaceans into two (Odontoceti and Mysticeti); primates into three (Lemuroidea, Simiae, and Tarsioidea); and artiodactyls into two (Tylopoda and Artiodactyla proper). The number of orders has thus increased from 18-19 to 30-31. None of these suggestions is yet well founded.

Further, mammalogists dealing with extensive paleontological material do not generally favor extreme division. An order is primarily regarded as an integrating and not a differentiating concept. Otherwise, there is the risk of a tendency, as in ornithological macrosystematics, for the concept of an order to become essentially indistinguishable from the concept of a family, and sometimes even simply substituted for it. As a result, the scientific aspect of the system of vertebrates has undoubtedly suffered, and is suffering even now, from the excessive

division of the system which sometimes uses the term 'fishlike vertebrates and fish'. From the established viewpoint, Duplicidentata are regarded as an independent order (Lagomorpha). Thus, we have here 19 instead of 18 orders. Of these, 10 or 52.6% are represented in our fauna. One, i.e., the sirenians (sea cow), is extinct.

The system of class adopted here is given below. The orders represented in the fauna of the USSR are marked with an asterisk. (V.H.)

CLASS MAMMALIA

Subclass PROTOTHERIA		Order MONOTREMATA
Subclass THERIA		
Infraclass METATHERIA		Order MARSUPIALIA
Infraclass EUTHERIA		
Cohort UNGUICULATA	—	[*Order INSECTIVORA Order DERMOPTERA *Order CHIROPTERA Order PRIMATES Order EDENTATA Order PHOLIDOTA]
Cohort GLIRES	—	[*Order LAGOMORPHA *Order RODENTIA]
Cohort MUTICA		*Order CETACEA
Cohort FERUNGULATA	—	[Superorder FERAEE — [*Order CARVINORA *Order PINNIPEDIA] Superorder PROTUNGULATA Order TUBULIDENTATA Superorder PAENUNGULATA — [Order PROBOSCIDEA Order HYRACOIDEA *Order SIRENIA] Superorder MESAXONIA *Order PERISSODACTYLA Superorder PARAXONIA *Order ARTIODACTYLA]

Key for Identifying Orders of Mammals [in the Soviet Union]

- 1 (2). Hind limbs absent. Body fishlike with large bilobate caudal fluke set horizontally **CETACEA.**
- 2 (1). Hind limbs present. Body not fishlike; tail, if present, not in the form of a bilobate fluke.
- 8 3 (4). Forelimbs in the form of leathery wings **CHIROPTERA.**
- 4 (3). Forelimbs of different structure.
- 5 (6). Fore- and hind limbs very short, paddle-shaped, and in the form of fins, i.e., all digits right up to very tips enclosed in a common skin **PINNIPEDIA.**
- 6 (5). Fore- and hind limbs of different structure, not in the form of fins.
- 7 (10). Hooves on legs.
- 8 (9). Only one hoof on each limb **PERISSODACTYLA.**¹
- 9 (8). Two large hooves and two small ones set above them occur on each limb **ARTIODACTYLA.**²
- 10 (7). Hooves absent on legs (claws present).
- 11 (14). Diastema occurs between large chisellike incisors and molars; its length not less than length of entire row of molars on the corresponding jaw. Canines absent.
- 12 (13). Two incisors on upper jaw **RODENTIA.**
- 13 (12). Four incisors on upper jaw; small blunt one occurs behind each of two large sharp ones **LAGOMORPHA.**
- 14 (11). Diastema between incisors and molars absent or much smaller than length of molar row. Canines present.
- 15 (16). Anterior portion of snout extends into well-developed small proboscis. Anteriormost tooth on each jaw or only on upper jaw much larger than adjacent tooth.³ **INSECTIVORA.**

¹ For description, see Vol. I.

² The structure of the limbs differs in camels. Each limb ends in two broad calloused pads and true hooves are absent, being replaced by two very broad claws. Camels are not included in this key because they are domesticated animals (the wild camel is extinct) (for description, see Vol. I).

³ If the tooth relation differs, the proboscis is always present; moreover, the forelimb is extremely short, the wrist very broad with huge claws and set on edge—inner surface backward (moles).

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- 16 (15). Anterior portion of snout does not form proboscis. Anterior-most tooth on each jaw not larger than adjacent tooth
 **CARNIVORA**⁴ (V.H.)

⁴ Skulls of the extinct Steller's cow, a representative of the order of sea cows or Sirenia, have been found on the coast of the Commander Islands. They are distinguished by the absence of teeth or even traces of them (alveoli) on either the upper or the lower jaw over a length of about 60 cm (for description, see Vol. II, Part 1).

ORDER OF PINNIPEDS

Order Pinnipedia Illiger, 1811

COHORT OF CARNIVORES AND HOOFED MAMMALS

COHORT Ferungulata Simpson, 1945

Superorder of Carnivores

Superorder FERAЕ Linnaeus, 1758

ORDER OF PINNIPEDS

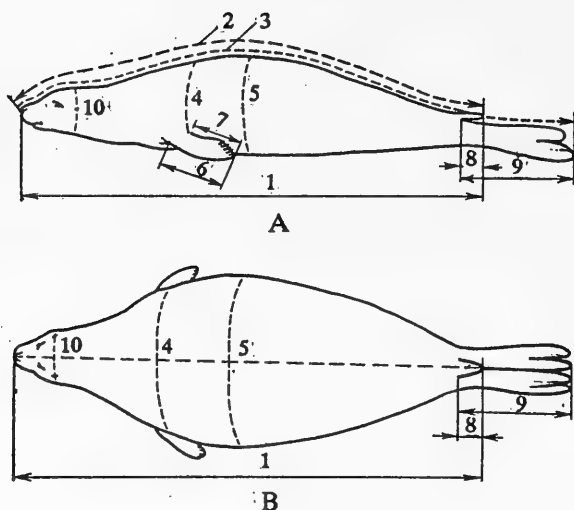
Order PINNIPEDIA Illiger, 1811¹

The order comprises mainly large mammals, morphologically well distinguished from the members of most of the other orders in their extreme adaptations to an aquatic mode of life.

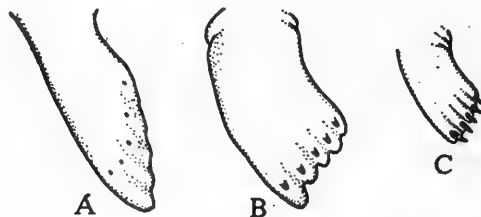
The body is somewhat spindle-shaped, streamlined, narrowed toward both ends, with an extremely poorly developed or even undeveloped tail (Fig. 1). Fore- and hind limbs are modified into oar-shaped paddles or flippers, with only their distal portions projecting from the cylindrical trunk and adapted for swimming. To a very small extent, these are used for resting upon and for moving on a solid substrate, but this faculty varies widely from family to family.

The fore- and hind limbs have five digits each. In some species (family of true or earless seals, Phocidae) claws are well developed on the fore flippers and, usually, on the hind flippers; in some species (all other families) claws are absent on the fore flippers but present on the hind flippers, though not in all species; in most species the claws are highly reduced, with almost imperceptible rudiments (Fig. 2). The hand with

¹ For reasons given (Vol. II, Part I, 1967, p. 53), Pinnipedia are regarded here as an independent order separated from the order Carnivora although such an interpretation is debatable. Weber (1928), Simpson (1945), Tenius and Hofer (1960), and some others, mainly paleontologists, regard Pinnipedia only as a suborder of Carnivora. (K. Ch.)



- 12 Fig. 1. Body shape and dimensions of Pinnipedia (seals): A—lateral view; B—dorsal view (K.K. Chapskii). 1—body length from anterior end of snout (nostrils) to tip of tail in a straight line (L_{cv}); 2—same, length along the dorsal surface (L_c); 3—total body length along the dorsal surface (with hind flippers, L_p); 4—axillary girth; 5—maximum girth; 6—length of fore flippers along outer edge; 7—same, length along the inner edge from axillary fold; 8—tail length; 9—length of hind flippers; 10—girth of head around the ear openings.



- 13 Fig. 2. Shape of fore flippers and disposition and growth of claws on them in the various families of Pinnipedia. A—eared seals (Otariidae); B—walruses (Odobenidae); C—true seals (Phocidae) (figure by K.K. Chapskii).

long digits is not separated externally into individual rays; the digits are covered with a web of skin, like a sheath, and set close together. The foot, too, has a similar structure. The phalanges bearing the claws are often slightly broadened and somewhat elongated with distinct gaps for nail beds or without them (Otariidae).

The scaphoid (scaphoideum), lunate (lunatum) and central (centrale) bones are fused in the carpus. The ulna and radius are

shortened but quite independent and not fused. The humerus is even more shortened, but bears a highly developed deltoid crest; the for. entepicondyloideum is seen in most cases but may be absent (even within the same species). The clavicle is not developed.

The digits of the feet are highly elongated. Among earless seals (Phocidae), however, the first and the fifth are particularly elongated (the fifth digit is also considerably broadened). All the digits have a thick web of skin joining them right up to the claws. In Phocidae, the elasticity of the web facilitates powerful movement of the digits. When stretched, the web forms a broad fan-shaped surface resembling the emarginate caudal fin of a fish (Fig. 3). The end phalanges of the extreme digits of the feet are quite broadened; in Phocidae, these have deep emarginate cavities for the claws.

The articular facet of the astragalus in true seals (Phocidae) is in the form of a sharply bulged crest but slightly concave in walruses (Odobenidae), and saddle-shaped in eared seals (Otariidae). The tibia is relatively long; the fibula is normally developed, totally independent, but fuses with the tibia in the proximal epiphysis in adults. The femur is highly shortened, flattened, and broadened distally; the third trochanter is absent; even the lesser trochanter is not developed in most cases.

The thoracic vertebrae usually number 15, the lumbar 5, and the sacral 4, while the caudal vary from 8 to 15. The vertebral column is extremely flexible with highly developed intervertebral cartilages.

The skull differs in shape and size. In most cases, the upper wall of the cranium is more or less distinctly flattened, while the sagittal crest is poorly developed or absent. The cerebral portion is capacious, while the facial portion is usually not longer than the cerebral but narrower and disposed below it, though sometimes only slightly so (walruses). The orbits are generally extremely broad and joined widely with the temporal fossa; with rare exceptions, the zygomatic arches are greatly shifted laterally while the interorbital space in most species is sharply constricted. The bony palate is compact (neglecting the anterior and posterior palatine fossae). The auditory bullae among many (Phocidae) are highly swollen and rounded, but more flattened and complex among others. The lachrymal bone is absent. The fossa pterygoidea is not developed. The alisphenoid canal is absent in true seals (Phocidae) but present in others (Fig. 4). The ethmoturbinal bones are small and arranged in five folds; the maxilloturbinal bones are usually highly developed and fill most of the nasal cavity.

The mandibular condyle is semicylindrical with a fairly distinct concavity (saddle-shaped) in the central part. The corresponding articular fossa in the basal part of the skull is transversely truncate, quite extended,

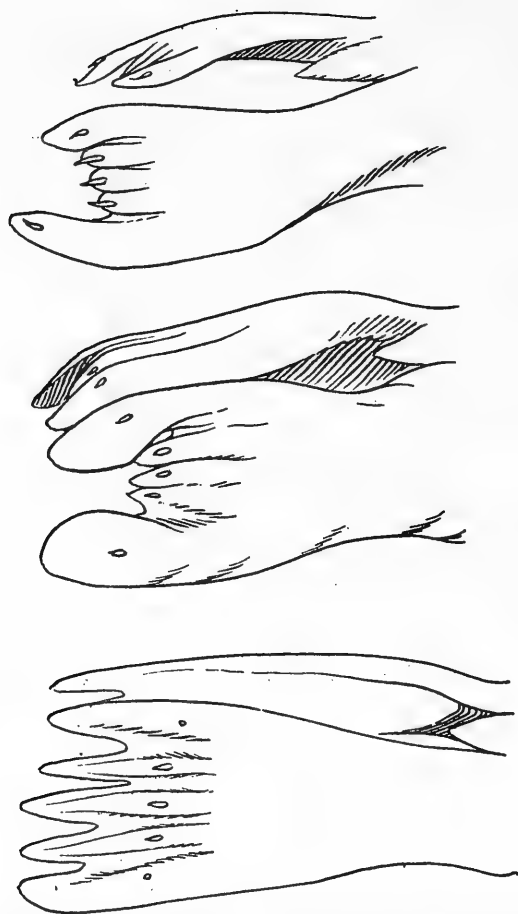


Fig. 3. Structure of hind flippers: (top to bottom)—true seals (Phocidae), walruses (Odobenidae), and eared seals (Otariidae) (figure by N.N. Kondakov).

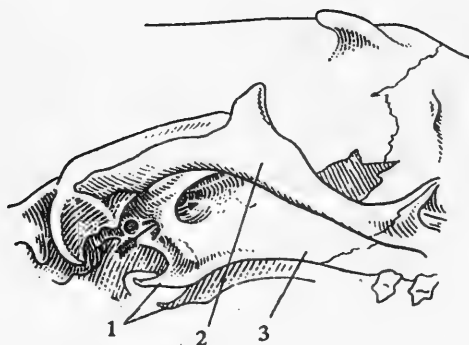
but of varying depth; however, neither its upper nor lower crests are so highly developed and flexed as to reach the mandibular condyle.

The Pinnipedia are heterodont but the carnassial teeth characteristic of predators (Carnivora) are not developed. The most common dental formula is:

$$I \frac{3}{2} \quad C \frac{1}{1} \quad P \frac{4}{4} \quad M \frac{1}{1} = 34.$$

The number of teeth is less in some seals and walruses. The more common permanent teeth formula among walruses is:

$$I \frac{1}{0} \quad C \frac{1}{1} \quad P \frac{3}{3} = 18.$$



14 Fig. 4. Disposition of alisphenoid canal (shown by an arrow) in the skull of Steller's sea lion *Eumetopias jubatus* (figure by N.N. Kondakov). 1—uncinate process of pterygoid; 2—zygomatic; 3—palatine bones.

The incisors in the lower jaw are relatively small, sometimes very weak; the lateral incisors in the upper jaw are highly developed as are the canines. The canines, especially the upper ones, are quite large; they are massive in walruses. The cheek teeth are less differentiated and usually flattened laterally. The structure of the crown is extremely diverse, in most cases with many cusps, but the main cusp is usually raised much above the others located behind and in front (or only behind). Monocuspids are not uncommon. The premolars have one or two roots; the true molar more often has two roots. Sometimes there is a diastema (or its analogue) between the fourth premolar and the molar.

The stomach is simple with a poorly developed cecum. The brain is microsmatic and relatively large. The hemispheres are highly furrowed with convolutions and four suprasylvian fissures.

The hair coat is variously developed: very dense in fur seals and in the newborn pups of almost all pagophilic species associated with ice. In an overwhelming majority of the species, it consists of three categories: fur, intermediary and guard hairs. In walruses, sea lions (genus *Zalophus*), and true seals (family Phocidae) (except the newborns) the hair coat is quite rough and relatively short, and the fur hairs very sparse with practically no underfur. The hair coat is sparsest in walruses and bearded seals (genus *Erignathus*). The tail is covered with hairs. The whiskers are well developed and are most abundant in walruses; among seals, these are most numerous in the bearded seal. The whiskers are longest in the eared seals [Otariidae]. The color of the hair coat is quite diverse; it is fairly monochromatic and dull in eared seals and walruses (Otarioidea) and mostly spotted in true seals (Phocidae) (in some of them with bright contrast). A fairly distinct color variation with age is characteristic of many.

The skin glands are normally developed but there are no special scent glands. Mammary glands occur on the ventral side of the body with one or two pairs of mammary teats. The testes are concealed under a subcutaneous adipose layer at the base of the hind flippers and are not externally visible in true seals. Some kind of scrotum is seen in eared seals (Otariidae), which is less developed in walruses. The copulatory organ is concealed in a preputial pouch under the skin in front of the testes; the preputial pore opens out ventrally between the navel and the anal orifice. An os penis is present. The genital opening in the female is disposed directly in front of the anus under a common skin fold. The uterus is bipartite. A rudimentary os clitoridis is present. The placenta is girdle-shaped (zonary) and deciduate.

Sexual dimorphism varies sharply. In polygamous species (eared seals, Otariidae; elephant seals, *Mirounga*; walruses; and some others) and also in hooded seals (*Cystophora*), the male is considerably larger than the female. Some other features of dimorphism are also evident in the male: processes of the nasal cavity in the form of a proboscis (trunk) or a hoodlike swelling (elephant and hooded seals), features of skin structure (tuberculate formations in the walrus), and some differences in the thickness and structure of the hair coat (fur seal, *Callorhinus*; sea lion, *Zalophus*). In many other species, differences are restricted to a somewhat more massive skull, powerful dental apparatus, in particular much larger canines, and some differences in color, size, and proportions of the body and skull.

Age related changes are quite significant. Pups differ from growing juveniles and the latter from adults in the structure and color of the hair coat; external sexual differences become prominent with age. Seasonal dimorphism is not developed. Molt occurs once, often with casting of the cornified layer of the epidermis.

The range of size differences among the various species of Pinnipedia is not particularly large. The smallest of them (ringed seal, *Phoca hispida*; Caspian seal, *Ph. caspica*; and females of the northern fur seal, *Callorhinus ursinus*) is rarely longer than 170 cm in adulthood (from tip of nose to end of tail dorsally, *Lc*) and usually weighs up to a hundred kilograms. However, the minimum body size of adults of individual populations is fairly low: the smallest of them, especially the Okhotsk ringed seal, is only a little over 1 m long (*Lc*) and weighs barely 20 kg. The largest of the Pinnipedia (elephant seals, *Mirounga*, and the male walrus) measure (*Lc*) up to 600 and 400 cm long and weigh 4-5 and 1.5 *
 15 tons respectively. The lower limit of weight is at least two-hundredths of the upper limit, which itself is somewhat (by at least one-fifth) less than the corresponding range for the order Carnivora.

In overall build, proportions and external appearance, biological types, forms of adaptations, and other features, Pinnipedia also do not exhibit as great a diversity as Carnivora. Adaptations to living in water and for overcoming its resistance during fast swimming have left a general imprint on the entire external appearance by evolving a streamlined body. Evolution proceeded mainly in two directions in developing the means of locomotion in water: 1) strengthening of the locomotor role of the hind limbs and 2) transfer of the main function of propulsion to the forelimbs. As a result, in some members of this group of mammals, i.e., true or earless seals (Phocidae), the hind flippers became more developed and adapted to serve as the main propeller in water; these flippers are turned backward and modified into paired caudal fins, similar to those of a fish. These are also broadened and emarginated distally. In the other group, eared seals (Otariidae), the fore flippers became the main source [organ] of propulsion and evolved into massive crested lobes, almost wholly devoid of a hair coat and claws. In this respect walruses occupy an intermediate position since, besides the powerful fore flippers, they also have hind flippers identical in structure with those of true seals, which actively participate in forward motion during swimming. The body curvature also plays a significant role in locomotion.

In conformity with the different types of locomotion in water, these two main groups of pinnipeds are differently adapted to moving on land. The hind flippers of true seals (Phocidae) do not bend forward and serve as a support on a hard substrate. The fore flippers are weak and also poorly adapted to movement on land. The animals rest on them and, clutching the ground with the claws, haul up the rest of the trunk in jerks and drag it along the ground. In this case their movement looks like typical spasmodic heaves or resembles somewhat that of geometrids [inch worms]: resting on the rear part of the body, they haul the front part forward and then, shifting the center of gravity to it and quite often clutching the substrate with the claws of the fore flippers, haul up the rear. In some species, for example the Caspian seal, the fore flippers of well-fed specimens are so small that they do not reach the ground. The alternation of points of support is rapid and hence advancement is not that slow but is short in duration—the animal soon becomes exhausted. Eared seals can rest on the hind flippers (bending forward at the ankle joint) as well as on the wrist of the fore flippers, and can shift from one foot to the other, though quite awkwardly, and thus hop. They can negotiate fairly steep rocky shores on which they climb with great agility in spite of the fact that their limbs are apparently poorly adapted for this purpose.

The bulkiest species, elephant seals (*Mirounga*) and walruses, move rather slowly on land. All the same, they exhibit extreme agility under

certain circumstances. Steller's sea lion can dive into water from a great height (Fig. 51). The animals swim in any position—on the back, side, or belly, in a submerged state or with the head above the water surface (or surfacing only periodically). Some are capable of jumping fairly high above the water (fur seals) but even the very heavy seals can leap from the water onto an ice floe in one jump.

Pinnipedia live in diverse climatic zones—arctic and antarctic, boreal and austral, and even subtropical. Depending on the season, they live in herds (often very large and dense) or in small isolated groups, singly or in pairs (for a short duration). In the wider sense of the word, not even
 16 one species can be regarded as a resident, including even those which are more confined to a given section or region. Somewhat developed migrations, or at least local wanderings, are typical of almost all the species of pinnipeds. Migrations in many species have a well-defined character (fur seal, Greenland seal, hooded seal, walrus, etc.) marked no less precisely than bird migrations, and extend over large distances (hundreds or even thousands of kilometers).

Despite all their adaptations to life in water, pinnipeds do require solid substrate on which they give birth, suckle the pups, molt, and in most cases mate, and simply rest. Some of them use only ice floes for this purpose (pagophilic² species and subspecies), while others select beaches, mostly of islands (aegialoid [beach or shore loving] or pagophob³ species and subspecies). As a rule, the more thermophilic species use the land (eared seals, Otariidae; subtropical seals with 8 incisors, Monachinae; and also some Phocinae with 10 incisors—true seals, and the West European form of gray seal). The rest of the 10-incisored seals, the hooded seal, and antarctic 8-incisored seals usually reproduce and molt on ice. Some pagophilic species (ringed and Baikal seals, Caspian seal, Greenland seal, and others) make round openings in the ice cover for breathing and ventilation, and for crawling onto the ice. Some burrow holes in the ice for themselves and for concealing their pups under the snow cover. There is no winter hibernation.

Polygamy is common to the aegialoid [littoral; pagophobic] pinnipeds. There is no strict monogamy since the males and females come together only for a short while, invariably preceded by fairly severe fights among the suitors. Males play no part in the care of the progeny.

Fertility is low: all pinnipeds usually deliver a single pup; twins are extremely rare. The newborns are large, fully formed, covered with a thick coat, with normally developed limbs and open eyes. Postnatal growth

² Ice-loving, according to the terminology of N.A. Smirnov (1914, 1927, and 1936).

³ Land-loving, ice-fearing species.

is quite rapid in some (hooded seal, Greenland seal, and most other pagophilic seals) and less so among others (Baikal seal, ringed seal). In some others, growth is very slow (walrus, fur seal, sea lion).

The feeding habits of pinnipeds are not clearly differentiated, though there are some mainly benthic feeders among them (walrus, *Odobenus*; bearded seal, *Erignathus*); some live on very large plankton, mostly fish and cephalopods (hooded seal; elephant seal; fur seals, *Callorhinus* and *Arctocephalus*; sea lion, *Zalophus*), and some live on planktonic crustaceans (crabeater, *Lobodon*). Most survive on mixed food consisting mostly of small and minute fishes, large plankton, some demersal crustaceans, as well as cephalopods and other mollusks. The leopard seal, *Hydrurga*, feeds also on large fish and warm-blooded animals, including birds (penguins).

Among the sense organs, the most developed are those of hearing and vision. The bony tympanic bullae are highly bulged in true seals (Phocidae) but flattened in all others. The pinnae are either altogether absent (true seals and walruses) or highly reduced (eared seals, Otariidae).

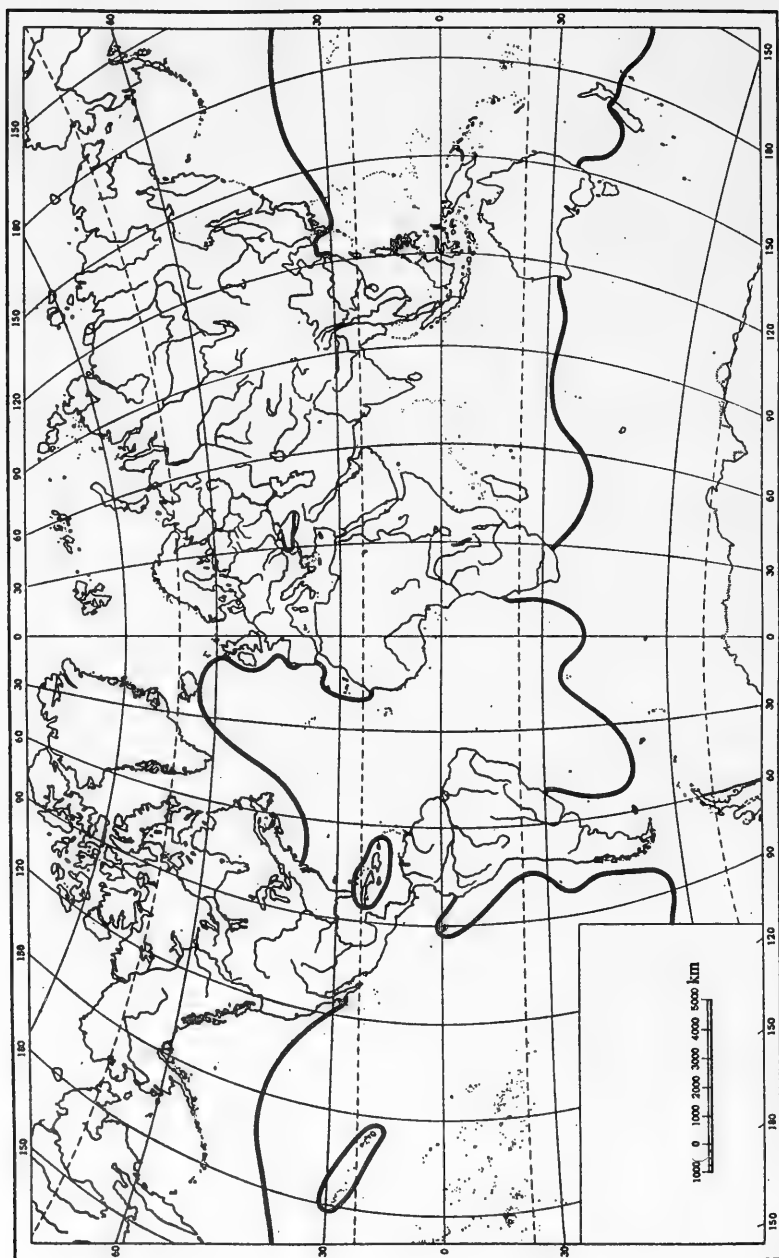
Pinnipeds are distributed in all the oceans except the Indian Ocean; they are found in the southernmost fringe of the latter (generally not above 30° S lat.) from the adjoining antarctic waters (Fig. 5).

18 An overwhelming majority of the species are confined to the regions of cold and moderately cold waters in which the surface temperature does not exceed 20° C at any time of the year (Davies, 1958b*). The exceptions are primarily thermophilic seals of the genus *Monachus*, with isolated distribution in three regions of the subtropical belt (one species in the Mediterranean Sea, in the open ocean around Gibraltar and Western Africa, and in the Black Sea; another in the Caribbean Sea⁴; and a third in the Hawaiian Islands). Many others can withstand relatively warm water conditions: the southern population of the northern elephant seals (*Mirounga* in California), the California, and Galapagos sea lions (*Zalophus*), the South African Cape fur seal (*Arctocephalus pusillus*), the South Australian and New Zealand eared seals of the genera *Neophoca*, *Phocartos*, and *Arctocephalus*, some populations of the northern elephant seal (*Mirounga angustirostris*), and others.

Pinnipeds are absent not only in the Indian Ocean but also in the Malayan archipelago, southwestern Pacific Ocean south of 30° N lat. to

* Here and throughout the text an asterisk (*) after a reference in the text indicates that either the author is not listed in the "Literature Cited" or the author is listed but no entry given for the publication date cited - General Editor.

⁴ The Caribbean monk seal (*Monachus tropicalis*) is extinct; the few survivors of its populations were finally exterminated in the first half of this century.



17 Fig. 5. Reconstructed range of the order Pinnipedia. Northern boundary in the Southern hemisphere and the Black Sea (K.K. Chapskii).

40° S lat., and in its entire central part south and north of the equator up to the 30th parallel. The only exception is the small area around the Hawaiian Islands occupied by the relict small population of the Hawaiian monk seal, *Monachus schauinslandi*. Pinnipeds are totally absent in the entire tropical portion of the Atlantic Ocean from 20° N lat. to 30° S lat. and some other pelagic parts of the world oceans, including a large expanse of temperate latitudes of the Atlantic to north of the equator (Figs. 5, 80).

At present, pinnipeds are most numerous in the boreal and arctic regions of the Northern hemisphere and in the temperate zone of the Southern, especially in the zones of confluence of cold and warm waters (zone "front," convergence).

Some 14 species inhabit the seas of the Arctic Ocean, northern and subarctic parts of the Atlantic, and the northern parts of the Pacific Ocean (mostly true seals with 10 incisors, i.e., Phocidae, walrus, and some eared seals); just as many species inhabit the waters of the Southern hemisphere (mostly eared and 8-incisored true seals). The remaining species are the above-mentioned subtropical monk seal and the inhabitants of landlocked waters such as the Caspian Sea and Lake Baikal.

The species most adapted to living in icy conditions (especially the ringed seal and to a lesser extent the bearded seal) penetrate into very high latitudes, into the Atlantic sector of the Arctic, and reach north of the 80th parallel and even the polar regions in eastern Severnaya Zemlya.

The zoogeographic range of pinnipeds is divided (Skleter,* 1897; and others) into five regions: 1) Arctoatlantic, including the Arctic Ocean and North Atlantic (endemic monotypic genera: hooded seals, *Cystophora*; gray seals, *Halichoerus*, to which may be added the Greenland seal); 2) Arctopacific, covering the extensive area of the North Pacific (endemic genera: northern fur seals, *Callorhinus*; sea lions, *Eumetopias*); 3) Mesatlantic (subtropical belt intersecting the Atlantic Ocean on both sides of the Tropic of Cancer and including the Mediterranean and Black seas)—area of distribution of the Caribbean and Mediterranean monk seals; 4) Mesopacific—similar to the small zone around the Hawaiian Islands where the third member of the genus of monk seals, *Monachus schauinslandi*, lives; and 5) Notopelagic—the zone encircling the Antarctic and extending north roughly along the 20°C isotherm of February surface temperature of the sea on the coasts of Chile and Peru and also covering the coastal waters of South Africa, South Australia, and New Zealand
19 (endemic genera: monotypic genera of the Antarctic, 8-incisored true seals—Phocidae; also the southern eared seals—Otariidae, especially the genera *Otaria*, *Neophoca*, *Phocarcos*, and many other species of southern fur seals of the genus *Arctocephalus*).

The general range of the order (Pinnipedia) did not undergo serious changes in the historic past, though in the eighteenth, nineteenth, and twentieth centuries significant "gaps" have been noticed. Some populations of the various species of southern fur seals (*Arctocephalus*) were totally exterminated and some of them, *A. philippi* (South America), almost completely. The Caribbean monk seal, *M. tropicalis*, has also become extinct in the present century while the Mediterranean species, *M. monachus*, is facing extinction.

The populations of many species have shrunk sharply while those of many others continue to shrink in the North and Arctoatlantic (common seal, *Phoca vitulina*; walrus and, at places, the gray seal, *Halichoerus grypus*; to a lesser extent populations of ringed seal, *Ph. hispida*, and some others) as also in the northern part of the Pacific Ocean (sea lion, *Zalophus californianus*; walrus); the population of the bearded seal, *Erignathus barbatus*, and of the ribbon seal, *Histiophoca fasciata*, has decreased sharply as a result of unrestrained hunting.

Conservation measures and a rational system of utilization have helped restore the populations. The population of the northern fur seal (*Callorhinus ursinus*) and that of the following southern fur seals have already reached high levels: *Arctocephalus pusillus* (in South Africa), *A. australis* (at the coasts of Uruguay and Argentina), and the elephant seal (*Mirounga leonina*) (especially on the island of South Georgia). Populations of the other southern fur seals and elephant seals as also the northern fur seal (at the Pacific coast of North America), which faced extinction, have begun to rise steadily.

The total world population of all the species of pinnipeds is estimated at 16-20 million. The maximum numbers exceeding 1 million are attributed to four species: 1) the antarctic crabeater seal, *Lobodon carcinophaga*, probably numbering 4-5 million; 2) the ringed seal, *Phoca hispida*, somewhat less numerous than the preceding species (1-2 million); 3) the Greenland seal, *Phoca groenlandica*, has a total population of 1.5-2 million; and 4) the northern fur seal, *Callorhinus ursinus*, has a total population of 2-2.5 million. The census of the southern sea lion, *Otaria byronia*, is estimated at 800,000, that of the southern elephant seal at 600,000, and for the bearded seal (*Erignathus barbatus*), hooded seal (*Cystophora cristata*), Weddell's seal (*Leptonychotes weddelli*), South African fur seal (*Arctocephalus pusillus*), and Caspian seal (*Phoca caspica*)—400,000-500,000 each. The population of most other species is even less (Chapskii, 1966; and others).

Phylogenetically, the Pinnipedia are very close to the Carnivora from whose more primitive ancestors they undoubtedly evolved comparatively recently (in the geological sense of time), but evidently not later than in

the Oligocene. In fact, members of this order belonging to the Oligocene have not yet been discovered. The oldest known fossils are from the Lower and Middle Miocene. These were fully formed members of the same families to which the present-day Pinnipedia belong. Thus, a member of the family of eared seals could be recognized from the lower jaw with teeth of the Lower Miocene seal, *Allodesmus kernensis* Kellogg. Similarly, the Middle Miocene genera *Leptophoca*, True, *Miophoca*, Zapfe, or the Upper Miocene genus *Monotherium* van Beneden belong to the family of true seals (Phocidae). At that time (if not earlier), the present-day subfamilies of Phocidae already existed.

The Miocene seals did not differ considerably from the present-day species and morphologically did not stand very close to any of the land or semiaquatic carnivores which could serve as the ancestral form for the evolution of pinnipeds. All this offers a basis for presuming that the initiation of the primary phyletic branches leading to the families of sea lions and fur seals (Otariidae), the walrus (Odobenidae), and true seals (Phocidae) should belong to a much earlier period than the Miocene.

Many cardinal differences in body structure between the eared (Otariidae) and earless (Phocidae) seals greatly complicate establishing a single root which could be regarded as the base for the evolution of this group of mammals. Among these characteristics are: features of the tarsal region (especially the structure of the ankle bone) and the resultant differences in the ability of the animals to move on land, difference in the general structure of flippers, numerous elements of craniological dissimilarity (structure of tympanic region, mastoid, its association with the paroccipital process, and presence or otherwise of the alisphenoid canal).

Quite some time ago (Maivart, 1885*) attention was drawn to the fact that one group of pinnipeds (eared seals and the walrus, Otarioidea) was significantly close to bears in many craniological features, while another group (true seals, Phocidae) reveals a similarity, though less distinctly, with martens. From this arose the concept of diphyletic origin (Kellogg, 1922; Howell, 1929,* 1930*; McLaren, 1960; Chapskii, 1963; King, 1964; and others).

In spite of some features complicating the adoption of this hypothesis, especially that bears represent a much younger branch of carnivores whose evolution is put in a much later period than Pinnipedia, the possible diphyletic origin of the latter is not excluded. The evolution of true seals (Phocidae) from martens is quite convincingly demonstrated by the find of a seallike otter—seal semantor, *Semantor macrurus*, in the Pliocene formations of Western Siberia (Orlov, 1931*). This animal possessed distinct transitional features of structure between the sea otter

and true seals. It was closer to the seal than the sea otter with respect to the humerus (Kirpichnikov, 1955), though some other skeletal elements have revealed, on the contrary, a very close genetic similarity with the sea otter (K.K. Chapskii). The historical evolution of true seals (Phocidae) evidently proceeded in a similar manner, but in a much earlier geological age. The semantor was a somewhat incomplete branch formed in the same direction, independent of the emerging seals, but under different conditions. This could serve as an argument in favor of the validity of different ways of formation of the different groups of Pinnipedia and, hence the possibility of interpreting the latter not as a phylogenetically valid order (or suborder) but as a composite group of animals arising from different roots.⁵

The extremely scant paleontological material on true seals in general, and especially the recent finds within the USSR, make it difficult to estimate the exact number of not only species, but even of genera of fossil Phocidae.

At present, 42 genera of Pinnipedia are known. Of these, 25 are fossil (Simpson, 1945; McLaren, 1960; Mitchell, 1961,* 1968*) and 17 Recent. This proportion does not, however, indicate that Pinnipedia are at the end of their evolutionary development. The Recent genera form a fairly large figure of 40%, which is much higher than the corresponding figure (28%) for the "contemporaneity" of land carnivores (Heptner *et al.*, 1967*).

The other indices from which the potentially developing state of the order could be judged are seen from the areas of distribution, population, and biological stability of the different species. The range of the common seal (*Phoca vitulina*) is very extensive and is interrupted only by ecological barriers; the range of the bearded seal (*Erignathus barbatus*), the ringed
21 seal (*Ph. hispida*), and the genus of southern fur seals (*Arctocephalus*) is fairly large though not continuous; the range of the northern fur seal (*Callorhinus ursinus*) and the Greenland seal (*P. groenlandica*) is also fairly large.

The relative diversity of forms in spite of the narrow specialization of the order as a whole is *per se* significant. The high population of many species (see above), including even such relict species as the Caspian seal existing under conditions of intense anthropogenic pressure, is an important feature. In spite of their low fertility, pinnipeds can quite quickly

⁵ The origin of a group or two highly proximate families of the same order (suborder) could hardly be regarded as polyphyly. This, at best, is paraphyly or a form of monophyly. (V.H.)

restore their populations and thus largely withstand destructive hunting. They cannot, however, survive incessant killing. Thus, one species (Caribbean monk seal, *Monachus tropicalis*) became totally extinct, while the population of another (Mediterranean monk seal, *M. monachus*) is vanishing right before our eyes; the population of yet another (Hawaiian monk seal, *M. schauinslandi*) is very small and only exists because of protective measures. Some other populations, especially of antarctic species, are in a pitiable state as a result of irrational killing. The population of all species of pinnipeds is wholly dependent on their judicious utilization and conservation.

The classification of the Pinnipedia is quite simple in its general features and more or less generally accepted. The differences arise only in the number and scope of systematic categories and the position of the entire group which is interpreted sometimes as an independent order or suborder of carnivores (Carnivora), and sometimes even as a composite group deserving a rank of several families (or subfamilies) in the superfamily Canoidea of carnivores (Carnivora). Moreover, none of the researchers inclined to such an interpretation (Friar, 1956*; Lien and Waiens, 1956*) have been able to specifically accomplish such an arrangement. The Pinnipedia, regarded as an independent order, are divided into two superfamilies: Otarioidea and Phocoidea. The former consists of two families: eared seals, Otariidae (Steller's sea lion, sea lions, and fur seals) and walruses, Odobenidae. The second superfamily comprises only a single family—true seals, Phocidae.⁶ Quite often (N.A. Smirnov, 1929, 1935; and others), only two families are recognized: Otariidae s. lato, which includes not only eared seals, but also walruses, and Phocidae, true seals.

Otarioidea are characterized by the following features: the bullae osseae are flattened and have complex angular outlines; the mastoid forms a single extremely massive process in adults; the process descends much below the tympanum part and fuses with the pr. paroccipitalis; the alisphenoid canal is present. The astragalus resembles more that of Carnivora than of members of Phocoidea. The hind limbs can bend forward and are adapted to locomotion on land.

Phocoidea are characterized by the following features: the tympanic bullae are fairly strongly bulged and rounded; the mastoid process is not joined with the pr. paroccipitalis (when present), not bent downward, and generally not well developed. The alisphenoid canal is absent. The astragalus has a large process at the top (no similarity whatsoever with

⁶ The fourth family, Semantoridae (fossils of seallike otter—semantors; Yu.A. Orlov, 1931), sometimes placed in the Pinnipedia (Simpson, 1945), should not be included here.

that in land carnivores) and its articular surface is not saddle-shaped. The hind limbs do not bend forward and do not participate at all in locomotion on land.

22 There is no basis for assuming that new species not known so far will be detected in the order.⁷ At the same time, the morphological features of the subspecies of many true seals (Phocidae) should be reviewed. The scope of some genera of this family should also be partly reviewed. However, there is hardly any need to revise the classical division of phocids into subfamilies, as recommended by King (1966). In the family of eared seals, Otariidae, there is evidently need for a more rational argument for the independence of all the species of the genus *Arctocephalus*.

Thus the system of eared seals of the Southern hemisphere at the level of genera and species cannot yet be regarded as conclusively established. There is no single opinion even about the scope of the genus of some northern seals of the subfamily Phocinae in view of the attempt of some theriologists to give a broader interpretation to the concept of genus. The antarctic 8-incisored seals can be regarded as conclusively established monotypic genera. The morpho-ecological rationale of changing the measurements of taxonomic differences prevailing among seals of the subgenera of the widely interpreted genus *Phoca* (true seals) is highly substantiated.

At present, 32-34 present-day species are included in the order Pinnipedia, i.e., only some 1% of the total number of species of mammals of the world. On average, a genus has 2.1 species. There are a maximum of 18-19 species in the family of true seals, Phocidae; eared seals, Otariidae, have 12-13 while there is only one species in the family of walruses, Odobenidae. The present-day pinniped fauna of the world is represented almost evenly in the North Atlantic basin (10 species including the Caspian seal), in the North Pacific Ocean (11-12 species) and in the seas of the Southern hemisphere (13 species).

Two superfamilies, all the 3 families, and 8 genera, i.e., 42% of the 19 present-day genera, are known in the seas and landlocked water bodies of the USSR. However, the fauna of the USSR comprises only 13 species,⁸ i.e., about 39% of all the species known in the world fauna.

⁷ The unexpected recent "discovery" in the Pacific Ocean of a "new" species, described under the name of the island seal *Phoca insularis* (Belkin, 1964), was actually one of the forms of the pagophobic common seal, *Phoca vitulina* (see p. 314, and also Chapskii, 1967, 1969).

⁸ If the common seal (*Phoca vitulina*) and the subspecies are regarded as a single species; see pp. 323-330.

The range of the order encompasses all the oceans of the USSR and some of the largest inland water bodies (Caspian Sea, Lake Baikal, Lake Ladoga).

The practical importance of pinnipeds is very high. Almost all the species, but primarily those which periodically form massive herds, represent game animals of great economic value and are hunted mainly for their fur and partly for their skin; the fat, meat, and some other body parts are also used.

Historically, the hunting of pinnipeds has played a major role. Sealing vessels combed the seas of both hemispheres in search of herds of these animals, especially fur seals, and killed them mercilessly. This carnage continued for decades and ultimately led to the near total depletion of stocks of the commercially valuable species. In the Southern hemisphere, all the rookeries of the southern fur seal were almost wholly ravaged and the elephant seal population suffered. The latter faced extinction even at very low latitudes. The rookeries of the northern fur seal on the Commander and Pribilof islands were subject to intense destruction. Effective conservation measures alone prevented the recurrence of the fate that befell many populations of the southern fur seal. The stocks of walrus were severely depleted, especially in the Atlantic sector of the Arctic, and also in other regions of its habitat.

In spite of its sordid history, sealing at sea has not lost its importance to date. In some regions of the globe it continues to play an important economic role as a supplier of raw material for the fur, hide, and other industries. In some countries (such as Greenland), sealing is extremely important and represents the only source of livelihood for northern native populations. Hunting of pinnipeds is of great significance in the life of the native coastal populations of Alaska and the Chukchi Peninsula, for the coastal villagers of the Soviet Arkhangel'sk region, and for hunters of some other regions of our country. It provides Eskimos and some coastal Chukchians meat for themselves and for their dogs, skin for making footwear, harnesses, and other requirements, as well as fat, etc. Moreover, it provides work for the people engaged at the collective farms and in the state-owned sealing industry.

In the USSR and many foreign countries, seal skins are in demand as highly valuable, durable, and fashionable furs. The most important targets of sealing are the northern and southern fur seals, the Greenland seal, the ringed seal, the Caspian seal, the hooded seal, etc. Fur is generally obtained from fur seals and mainly young Greenland and Caspian seals, hooded seals, etc., while the skin is obtained from large animals. Blubber is mainly used commercially in the tanning industry,

for soap-making, etc., for making medicinal ("fish") oil, and as an ingredient in other products. Meat is used locally. Some pinnipeds (e.g., large seals) inflict much damage in fisheries by thriving on prime fish, especially salmon. The most important commercial species of seals are now exploited almost everywhere on a rational basis, eliminating the danger of their depletion. (K. Ch.)

Key to Families of Pinnipedia

Identification Based on External Features

- 1 (4). Hind flippers bent at calcaneal joint with foot forward, serving as body support on hard ground. Fore flippers longer than hind ones, naked distally; claws on hands absent or poorly developed and placed well behind margin.
- 2 (3). Snout narrowed anteriorly and quite elongated; pinnae small. Hands long, roughly triangular, wing-shaped. Claws absent (or very small). Well-developed claws only on three middle digits of hind flippers. Upper canines (in adults) not protruding from closed mouth. Eared seals, Otariidae (p. 58)
- 3 (2). Snout very broad, anteriorly somewhat truncated and short. Traces of pinnae not seen. Hands not highly elongated and not triangular; small reduced claws seen on digits of hands and all digits of feet. Upper canines notably protruding from closed mouth. Walruses, Odobenidae (p. 22)
- 4 (1). Hind flippers not bent forward at calcaneal joint, always held backward, and not serving as body support on solid ground. Fore flippers not long, slightly shorter than hind ones, and fully covered with fur. Hand with well-developed claws at end of digits. True seals, Phocidae (p. 142)

Identification Based on Skull Features

- 1 (4). Tympanic bullae relatively small, flattened from top downward, with uneven rugose surface, and complex outline. Alisphenoid canal (Fig. 4) present. Mastoid part of temporals with very massive protuberance directed downward. All or almost all cheek teeth with single root (the last with two roots) and with simple undivided crown.
- 2 (3). Rostral portion [of skull] slightly narrower than cranial part in temporal region. Ends of middle pair of upper incisors with transverse angular notch (Fig. 6). Nasals shifted backward and projection of frontals lodged in fork between their apices (Fig. 7). Supraorbital processes well developed. Lower jaw teeth sharply differentiated

25

into incisors, canines, and cheek teeth (premolars and molars similar). Upper canines similar to lower ones in size and structure.

..... Eared seals, Otariidae (p. 58)

- 3 (2). Rostral portion [of skull] hardly less wide than cranial portion in temporal region. Ends of nasals posteriorly, at junction with frontals, sharply incised transversely, not forming acute apices (Fig. 7). Supraorbital processes not developed. Lower jaw teeth similar to one another; upper canines large and may attain large size, bearing no similarity to the lower ones, which do not differ from cheek teeth. Walruses, Odobenidae (p. 22)

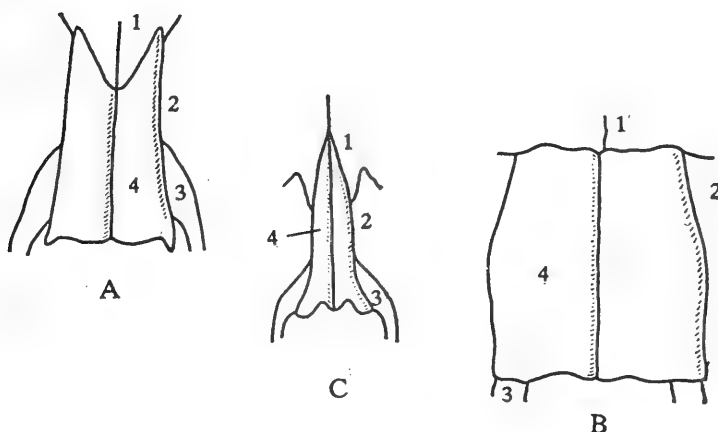
- 4 (1). Tympanic bullae relatively large, bulging, with almost smooth semicircular surface and comparatively simple outline. Alisphenoid canal absent. Mastoid part of temporals without massive downwardly directed protuberance. Most cheek teeth with two roots and with divided crown.

..... True seals, Phocidae (p. 142). (K. Ch.)



24

Fig. 6. Transverse notch in middle upper incisor of eared seals, Otariidae, and the fur seal, *Callorhinus ursinus* (figure by K.K. Chapskii).



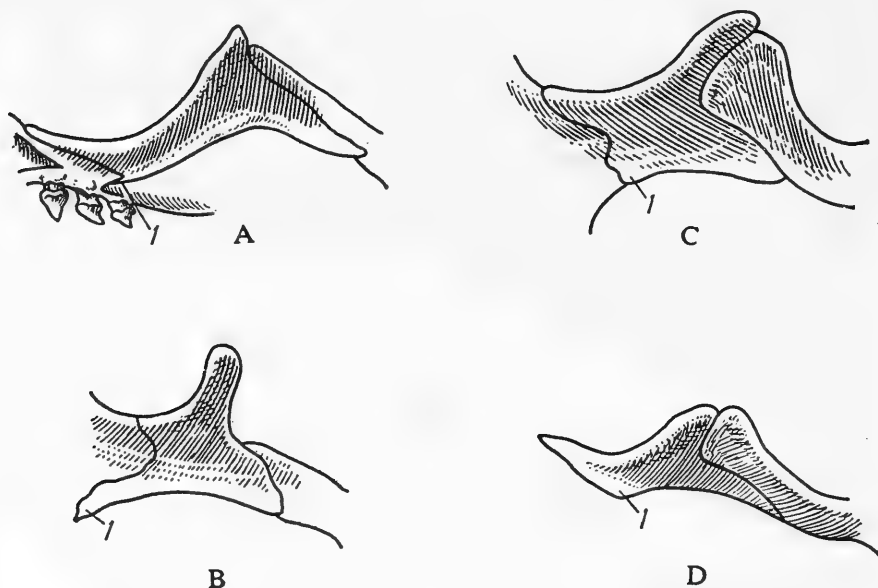
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Fig. 7. Structure of nasals in pinnipeds of various families: A—eared seals (family Otariidae); B—walruses (family Odobenidae); C—true seals (family Phocidae): 1—frontal, 2—maxillary, 3—premaxillary, 4—nasal bones.

Family of Walruses

Family ODOBENIDAE Allen, 1880

This is one of the largest groups of animals of the order Pinnipedia. The trunk is massive; the head is rounded and, compared with the massive body, appears small. Pinnae are absent. The whiskers are long, dense,



24 Fig. 8. Left zygomatic bone in pinnipeds: A—eared seal (fur seal, *Callorhinus ursinus*); B—walrus (*Odobenus rosmarus*); C—bearded seal (*Erignathus barbatus*); D—common seal (*Phoca vitulina*) (figures by K.K. Chapskii):
1—anterior lower corner (or process).

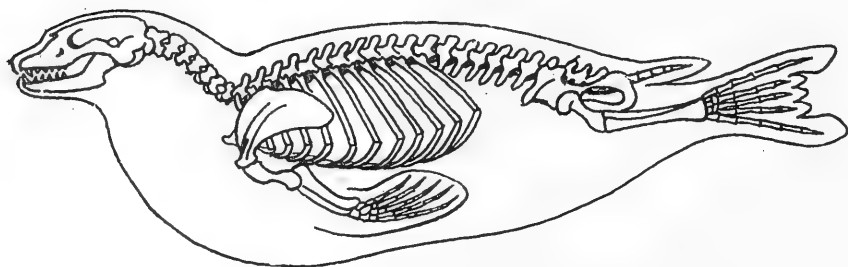


Fig. 9. Skeleton of a seal (figure by N.S. Kondakov).

very thick, and directed downward. The neck is short but movable and merges imperceptibly into a fairly clumsy trunk. The skin is thick, rough, and forms numerous folds and wrinkles. The hair coat is sparse and bristly; large portions of the body are naked in adults.

The fore flippers are slightly larger than the hind ones, terminating in a frill of skin devoid of hair; the frill extends beyond the margin of the digital phalanges. The first digit (inner) is the longest and the rest shorter in the order of first to fifth. The hind flippers have a naked foot; the fifth digit is the longest; the first is almost equal to it. The claws on the flippers are weakly developed and disposed away from the margin of the flippers. The hind flippers can bend under the trunk and assist in movement on land (Fig. 10).

There is one pair of teats. The testes are disposed under a layer of skin and fat (subintegumental); a scrotum is absent.

The skull is massive and broad with an extremely massive elevated frontal portion, by which it differs from the skulls of all other Pinnipedia (Fig. 11). The skull bones are highly massive. The width of the skull above the canines is almost equal to the width above the external auditory meatus. A supraorbital process is absent. The hind margin of the nasals forms an almost straight line. The orbits are relatively small, their transverse width equal to $1/3$ or $1/2$ the width of the palate in the line of molars. The bony palate is flexed inward like a boat, forming at the back a very gentle arc turned forward with a bulge. The external auditory meatuses are very small and their lower walls thickened.

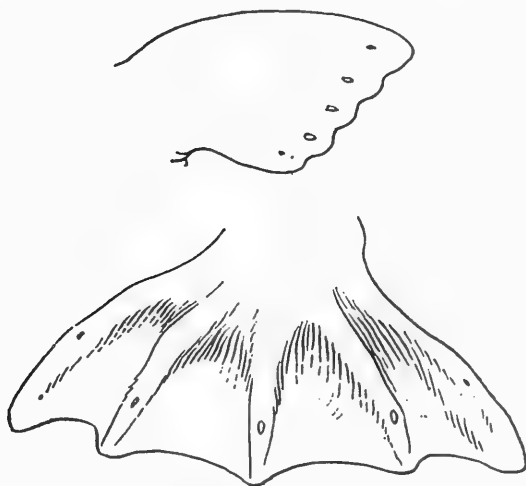


Fig. 10. Fore and hind limbs of the walrus (figure by N.N. Kondakov).

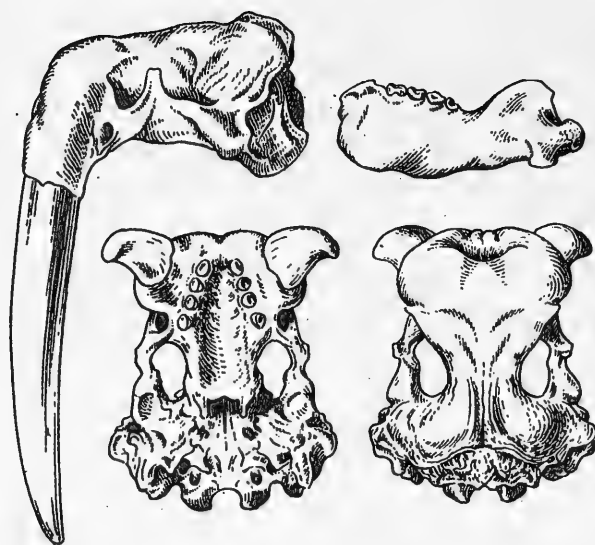


Fig. 11. Skull of an adult walrus, *Odobenus rosmarus* (figure by N.N. Kondakov).

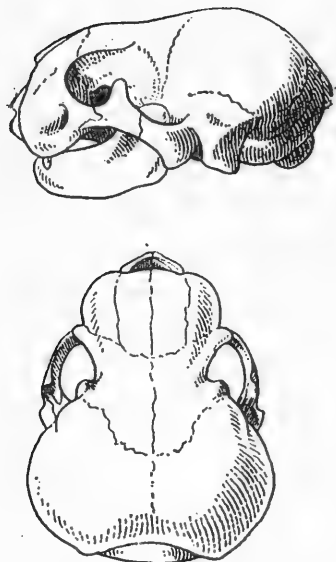
The tympanic bullae are relatively small and flattened. The lower lateral angle of the temporal bone bears a massive projection. This bony mass exceeds the height of the tympanic bulla by a few times. The anterior section of the lower jaw is very massive and its two halves are firmly fused. The dental formula of permanent teeth in most walruses is:

$$I \frac{2-2}{0-0} \text{ or } \frac{1-1}{0-0}; \quad C \frac{1-1}{1-1}; \quad M \frac{3-3}{3-3}.$$

The front incisors are small or altogether reduced, while the last pair of incisors is indistinguishable from the molars in size and shape. The upper canines are massive, up to 80 cm long, and directed vertically downward. The molars are massive, with a single root, their cusps sloping backward. In older animals the molars become worn and flat, and even have a slightly concave surface.

The scapula is relatively long, without a perceptible arcuate notch on the hind margin. Its crest is comparatively elongated, reaching the hind margin. The os penis is very long, 508-512 mm, slightly S-shaped, its posterior end broadened and terminating in a head; the anterior end is obliquely truncated.

- 27 Paired air sacs are formed by a projection of the upper section of the esophagus and the broad openings joined with it. There are no closing valves. Each sac can hold up to 50 liters of water [air]. The



26 Fig. 12. Skull of a yearling walrus, *Odobenus rosmarus* (figure by N.N. Kondakov).

air-filled sacs inflate and, spreading under the skin of the neck, hold it up; their ends lie between the scapulae (Sleptsov, 1940; Nikulin, 1941; Fay, 1960*).

Walruses mainly inhabit the coastal shallow waters of arctic seas and feed on benthic invertebrates. A large part of their life is associated with ice floes.

Walruses are distributed only in the Northern hemisphere, in the circumpolar region, with small interruptions. They inhabit the Bering, Chukchi, East Siberian, Laptev, Kara, and Barents seas and the waters of the Canadian archipelago in the northwestern part of the North Atlantic Ocean.

Walruses constitute one of the three families of the order Pinnipedia, but the taxonomic position of the family has not yet been clearly established. Some authors regard it as a subfamily of the family Otariidae (Smirnov, 1935; Romer, 1939; and others), while many separate it into an independent family. The latter view is more prevalent.

The relative proximity of the family of walruses to eared seals (Otariidae) is, however, beyond doubt. This fact is particularly emphasized by combining them into one superfamily, Otarioidea Smirnov, and contrasting them in such a combined form with the superfamily Phocoidea Smirnov, comprising only the family of true seals.

In origin, the walrus family is closely related to the family of eared seals (Otariidae) and could be regarded as its derivative. Thus the earliest and most primitive known form of the walrus family, *Prorosmarus alleni*, from the Upper Miocene of the Atlantic coast of North America bears some features of the skull structure and dentition characteristic of Otariidae. In particular, the lower canines are preserved in this form (Tenius and Gofer, 1960*).

Of the four genera of the family, only one is Recent. Apart from *Prorosmarus*, two other genera, i.e., *Trichechodon* and *Alachtherium*, are known from the Middle Pliocene and Pleistocene of Europe. The only present-day genus, *Odobenus*, is known from the Pleistocene of North America and Europe. Extinct as well as extant genera are known only from the arctic seas of the European and American continents, i.e., the present-day range of the family. The North Atlantic Ocean could perhaps be regarded as the center of origin of this family.

The economic importance of this family is presently low, since the walrus population has been greatly depleted in recent decades.

The family is represented by one genus, *Odobenus* Brisson, 1762, with a single species, *O. rosmarus* Linnaeus, 1758, widely distributed in the waters of the USSR. (V.A.)

Genus of Walruses

Genus *Odobenus* Brisson, 1762

- 1762. *Odobenus*. Brisson. Regnum animale. Ed. 2, p. 30. *Phoca rosmarus* Linnaeus.
- 1766. *Trichechus*. Linnaeus. Syst. Nat., ed. XII, I, p. 49. Nec Linnaeus 1758 (pertains to manatee *Trichechus manatus* Linnaeus, 1758).
- 1772. *Rosmarus*. Brünnich. Zoologiae fundamenta, p. 34. *Phoca rosmarus* Linnaeus, 1758. (V.H.)
See description of the family.

WALRUS

Odobenus rosmarus (Linnaeus, 1758)

- 1758. *Phoca rosmarus*. Linnaeus. Syst. nat. Ed. X, I, p. 38, North Atlantic Ocean.
- 1811. *Trichechus arcticus*. Pallas. Zoogr. rosso-asiatica, I, p. 269, Novaya Zemlya ("Frequens in Oceano arctico ... Copiosissimi in Insula Navaja Zemla." (V.H.)

1815. *Trichechus divergens*. Illiger. Abh. Acad. Wiss. Berlin, 1804—II, p. 68. 35 miles south of Ici Cape, Alaska (162° W long. and 70° N lat.), Chukchi Sea. (V.H.)
1815. *Trichechus obesus*. Illiger. Ibid., p. 64, Nom. nud.
1831. *Trichechus cookii*. Fremery. Bijdrag. Nat. Vetensk, 6, p. 385. Ici Cape zone in Alaska (Chukchi Sea, 70° N lat. and 163° 18' W long.).
1922. *Trichechus orientalis*. Dybowski. Arch. Tow. Nauk. Lwow., I, p. 351, Nom. nud.
1940. *Odobenus rosmarus laptevi*. Chapskij. "Problemy Arktiki" (Problems of the Arctic), No. 6, p. 94. Laptev Sea. (V.H.)

Diagnosis

Only species of the genus.

Description

In general form, the walrus differs considerably from all other species of Pinnipedia (Fig. 13). The body is large and massive, the skin thick, covered with wrinkles and folds, and the limbs broad (Fig. 13). Movement on land is slow and cumbersome and the animal utilizes all four limbs, but in water it is quite agile and moves fairly fast. It crawls onto ice floes with difficulty, using its tusks and fore flippers.

- 29 The head is relatively small with a massive snout that is blunt in front. The eyes are small and shifted far back (Fig. 14). Long (up to 10-12 cm), numerous, very hard and thick whiskers occur on the front part of the snout; they are directed downward and arranged in 13-14 rows. Each side of the snout bears 300-350 whiskers. The whiskers in the middle part of the snout are usually very worn and measure hardly 0.5 to 1 cm.

Both tusks in the upper jaw are very long and directed vertically downward. Instances are known of walruses with more than one pair of tusks. A walrus caught around 1915 had two well-developed tusks on each side, and all four were of almost normal length. Those on the right side grew parallel to each other while those on the left were twisted (Caldwell, 1964). Four skulls have been described with three tusks and five with five tusks each. A skull was found in which there was a single normally developed tusk on the left and five separate formations on the right side consisting of fragments of small tusks of normal shape, two dentine stubs 12 and 14 cm long rising from the surface of the gums, and two dentine concretions 12 and 20 mm in diameter concealed in the jawbone (Bel'kovich and Yablokov, 1960).



Fig. 13. A group of walrus of different ages (figure by N.N. Kondakov).

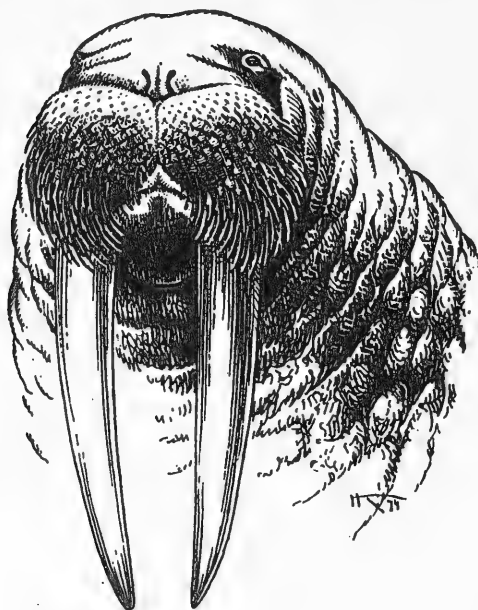


Fig. 14. Front view of a walrus head (figure by N.N. Kondakov).

The color of old walruses is a dirty olive on the back and rusty-brown on the belly. This coloration is caused by the color of the hair, as also the skin pigmentation, which is brownish. The tips of the flippers, devoid of hair, are similar in coloration.

Sexual and age-related dimorphism are manifest in the body dimensions, shape and size of tusks, and hair coat. Adult males are about 0.5 m longer than females; the male skull is more massive and the tusks longer and thicker than in the female. The tips of the tusks diverge sideways in the male but in the female are somewhat proximate with a slightly spiral curvature. The female, usually darker, attains maturity one to two years earlier than the male. Pups of both sexes are identical in size, but the female lags behind in growth during the period of sexual maturity and ceases to grow altogether soon thereafter; cessation of growth sets in later in the male. A clear example of sexual dimorphism is the presence of large wartlike formations on the breast and shoulders of males, which are absent in mature females.

The hair coat of young walruses is fairly dense and dark brown. It becomes bristly, sparse, and brownish-yellow with age, with large bald patches. Evidently the hair color undergoes no seasonal variations. (For skull description, see under characteristics of the family; body and skull sizes are given under "Geographic Variation".) The weight of an adult male can reach almost 1,500 kg and that of an adult female 800-900 kg. The average weight of the visceral organs (seven specimens) is: heart 6,167 g, lungs 14,062 g, liver 29,640 g, spleen 4,146 g, stomach 5,312 g, intestine 33,640 g, kidneys 3,544 g, and pancreas 2,148 g. (V.A.)

Geographic Distribution

Arctic seas of the Atlantic and Pacific Oceans.

Geographic Range in the USSR (Reconstructed)

In the early twentieth century, walruses were probably regular inhabitants of the northern White Sea (Morzhovets Island). In the Bering Sea during the nineteenth century, walruses bred regularly on Karaginsk Island (59° N lat.) and in the 1880s were caught in thousands every year. Walruses were reported on Cape Kronotskii (56° N lat.), Cape Shipunskii (53° N lat.), and on the Commander Islands (Grebnskii, 1902; Suvorov, 1914; Arsen'ev, 1928*; Ognev, 1935; N. Smirnov, 1935; Nikulin, 1941) (Fig. 15).

Direct references are available to the breeding of walruses in the northern part of the Sea of Okhotsk. The reports of a Yakutian army commander in 1651 refer to the hunting possibilities of walruses in the

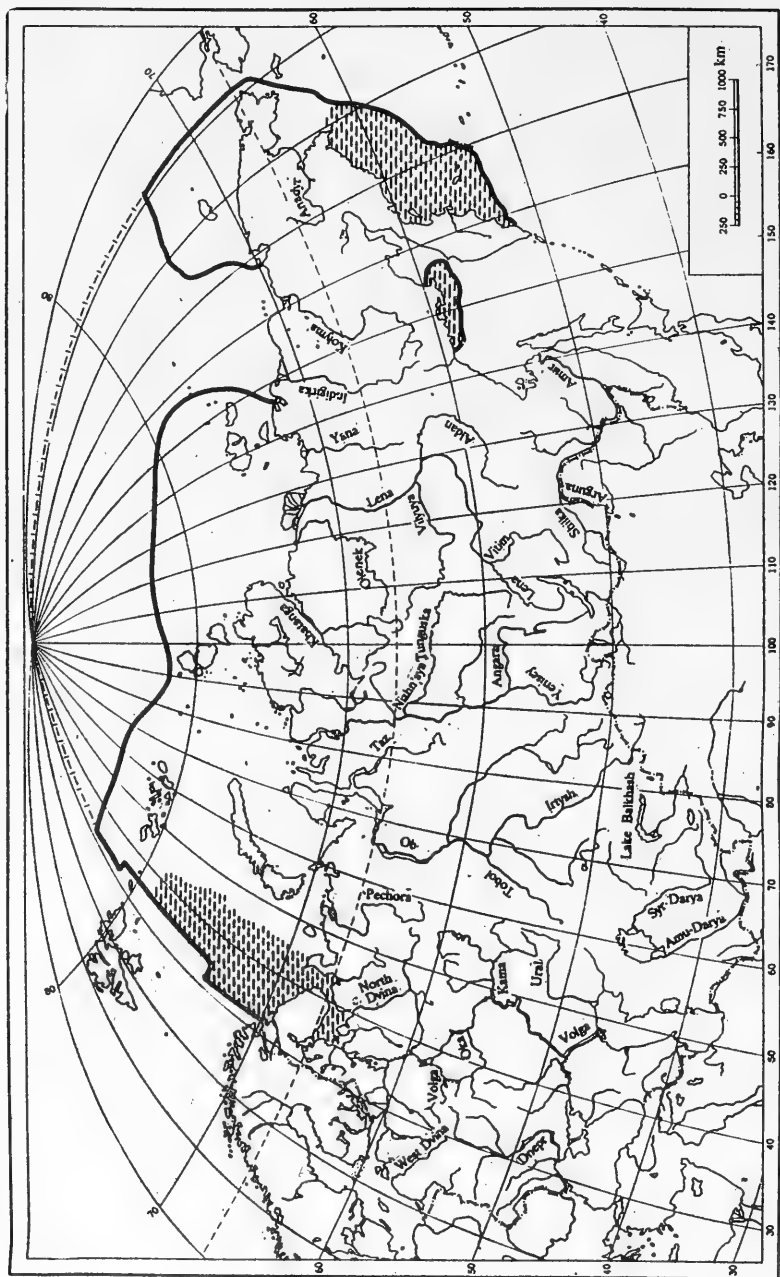


Fig. 15. Distribution of the walrus, *Odobenus rosmarus*, in the USSR (V.A. Arsen'ev). Solid line denotes the boundary of the reconstructed range and hatched zones the regions in which the walrus is now extinct.

Sea of Okhotsk. In the record for 1652, he reported sighting many walruses on the beach of Cape Morzhov for two or more "versts" [1 verst = 1.067 km] (Akinfov, 1848). These data pertain to the northern part of the Sea of Okhotsk not far from the present Magadan. (V.A.) The veracity of this report was confirmed by a reference to the possibility of finding "fish teeth," i.e., walrus tusks, at these places. This is also supported by the find of tusks in the coastal rock mounds along the northern coast of the Sea of Okhotsk, and the sighting of live walruses. A young walrus was found around 1890 on Yamsk Island in the northeastern part of the Sea of Okhotsk and a pair of tusks was found around 1900 on the coastal dumps of Shelikhov Strait. Walrus tusks were also found in Nogaev Bay (B.A. Zenkovich).

The present-day distribution of walruses in the USSR forms but a small part of the range which prevailed in the past. Walruses inhabit the waters of Franz Josef Land, Novaya Zemlya, Barents and Kara seas, Severnaya Zemlya islands (more often on the eastern coast of the archipelago), Vil'kitsk Strait, and in the shallow waters of the Ob'-Yenisey. They inhabit the Laptev Sea (mostly its western part close to the eastern Taimyr coast), Lena delta, landlocked waters of the Novosibirsk archipelago (mostly its northwestern fringe), and are encountered in the western part of the East Siberian Sea, mainly in the region of Novosibirsk Islands and De Long Islands. Farther east, they are found in the Chukchi Sea from De Long Strait in the west to Wrangel Island in the north, Bering Strait and Anadyr Strait to Cape Navarin (Chapskii, 1936, 1939, 1940, 1941, 1963; Tsalkin, 1937; Belopol'skii, 1939; L.N. Popov, 1939; Rutilevskii, 1939; Nikulin, 1941; Vinogradov, 1949; Zakharov, 1958; L.A. Popov, 1958, 1959, 1960).

Geographic Range outside the USSR (Reconstructed)

The southern boundary of walrus distribution in the Atlantic Ocean outside the waters of the USSR has also varied considerably. Judging from the finds of walrus remains in excavations, this animal penetrated far southward at one time. In the nineteenth century, its remains were found in Denmark, England, France, and on the east coast of North America in New Jersey, Virginia, and Carolina (Moor, 1952*). Instances are known of the discovery of walrus remains in Maine and Massachusetts. Moreover, fragments of the skull and other bones were found in the Gulf of Maine (G.M. Allen, 1930; Palmer, 1944). In the first half of the seventeenth century, walrus hunting prevailed on Sable Island (44° N lat.), close to the Canadian coast north of the Gulf of Maine (G.M. Allen, 1930) and on the Magdalen Islands (Mansfield, 1959).

In the middle of the nineteenth century, stray walruses were caught on the Shetland and Orkney islands (Moor, 1952*). At the end of the nineteenth century, walruses were perhaps permanent inhabitants on the coast of Finmarken in northern Norway, found on the coasts of Scotland, and in the Gulf of St. Lawrence. In general, at the end of the last century, walruses were widely distributed in the northern part of the Atlantic Ocean and in the Arctic Sea.

- 33 It has been assumed that in the eastern part of the Pacific Ocean, walruses penetrated south of the Aleutian Islands, reaching Shumagin Island and even the Alexander archipelago in the eastern part of the Gulf of Alaska.

In the middle of this century, walruses were known to inhabit the northern part of the Atlantic Ocean, being recorded in the waters of the Canadian archipelago (Southampton and Devon islands, Fox Basin, and Baffin Bay), the Labrador coast, Davis Strait, the west and east coasts of Greenland, Spitsbergen, and were sometimes spotted near Iceland (Fig. 16).

In the Pacific Ocean, walruses inhabit the eastern part of the Bering Sea, from Bristol Bay in the south to the Bering Strait in the north (including the St. Lawrence Islands, Nunivak, and St. Matthew), and extend along the north coast of Alaska into the Chukchi Sea up to Cape Barrow.

The northern boundary of the range of walruses in the Barents and Kara seas runs beyond 80° N lat. In April, 1957, a walrus was noticed in the breeding grounds on Franz Josef Land north of 81° N lat. (Vaigachev, 1958). In the waters of the Pacific Basin, the area 72 to 74° N lat. can be regarded as the regular northern boundary of the range of walruses, but the animals can be found even more northward in favorable years, depending on the situation of the ice floes. (V.A.)

Geographic Variation

Usually, three subspecies are recognized. All of them inhabit the waters of the USSR.

1. **Atlantic walrus** (*O. r. rosmarus* (Linnaeus, 1758)) (syn. *arcticus*, ? *obesus*).

This is the smallest form.

The maximum body length of males is 375 cm, of females 338 cm; the corresponding averages are 345 and 293 cm respectively (Chapskii, 1963). The condylobasal length of skull in males is 256-379 mm (\bar{x} = 369), in females 303-342 mm (\bar{x} = 314); the maximum width of skull in males is 268-291 mm, in females 222-257 mm (\bar{x} = 234.2). The length of male tusks along the curvature from the edge of the alveolus to the



Fig. 16. Distribution of the walrus, *Odobenus rosmarus* (V.A. Arsen'ev). 1—boundary of reconstructed range; 2—regions in which walruses are now extinct; 3—sites of present-day finds of walruses; 4—sites of finds of walrus fossils.

tip is 34-38 cm, in females 27-33 cm (Ognev, 1935). The tusk length in one male was 52.5 cm (Chapskii, 1963).

In the USSR it inhabits the Barents and Kara seas; outside the USSR, the North Atlantic Ocean to the Canadian archipelago in the west, inclusive.

2. *Laptev walrus* (*O. r. laptevi* Chapsky, 1940).

Somewhat larger than the Atlantic form.

The maximum body length of males is 410 cm, of females 370 cm; maximum length of the tusk is 65 cm in males, in females 58 cm. The maximum circumference of the tusk in males is 21 cm, in females 14 cm (L.A. Popov, 1960).

This form inhabits the Laptev Sea, the western part of the East Siberian Sea, the Lena Delta, and the Novosibirsk archipelago. It is more numerous near the coast of eastern Taimyr, where it is mainly confined to the coastal region and the shallow waters; it is rare in the western part of the East Siberian Sea in the region bordering the Laptev Sea.

Not found outside the USSR waters.

3. *Pacific walrus* (*O. r. divergens* (Illiger, 1815)) (syn. *cookii*, ? *orientalis*).

Largest form of the species.

The maximum body length of males is 450 cm ($\bar{x} = 336$), of females 367 cm ($\bar{x} = 283$). The skull is more massive than in other forms and the frontal section considerably broader. The condylobasal length of the skull in males is 383-428 mm ($\bar{x} = 396.8$), in females 315-357 mm ($\bar{x} = 332$); maximum width of the skull in males is 290-333 mm ($\bar{x} = 309$), in females 219-265 mm ($\bar{x} = 245$). The length of the tusk in males is 46-80 cm, in females 40-60 cm; its width in males is 66-84 mm, in females 41-53 mm (Ognev, 1935; Nikulin, 1941; Freiman, 1941).

34 It inhabits the Bering, Chukchi, and eastern part of the East Siberian seas. Some contacts between the Pacific, Laptev, and East Siberian Sea walruses are possible.

Outside the USSR, it is found in American waters of the Bering and Chukchi seas. (V.A.)

Biology

Population. As a result of prolonged hunting, the walrus population has declined steeply throughout its range.

The population of the Atlantic walrus has suffered the most and only a few stray herds are now known. The walruses of the Kara Sea suffered the highest destruction and those remaining now do not exceed a few thousand. Small groups are confined to Franz Josef Land

and Spitsbergen. The population in the eastern part of the Canadian archipelago is split into a few groups. In the northern part of Hudson Bay and in the region of Southampton and Cox, some 3,000 are known (Mansfield, 1959). Population figures for other regions are not available.

The population of the Laptev Sea walrus has been less affected by exploitation, as it has always been relatively small. Nevertheless, hunting has had its impact here as well, and the present population barely exceeds 5,000-6,000.

The Pacific walrus populations are best protected. Aerovisual estimates, aerial photographs, and studies of coastal breeding grounds and rookeries on the icy coasts revealed a summer population of 30,000-35,000 in the USSR. According to American and Canadian authorities, some 15,000 walrus inhabit the US waters in summer. The total population thus is 50,000 (Fay, 1957; Fedoseev, 1962; Krylov, 1968; Gol'tsev, 1968).

Habitat. An outstanding feature of the habitat is the relatively shallow water and abundance of benthic mollusks and partly of crustaceans. Drifting ice is common in these sections and, in the winter months, walrus inhabit only the ice (Fig. 18). In the absence of ice in summer, walrus form coastal rookeries mainly on sandy or pebbly shoals on the coasts of the continent or islands.

Food. There is no information on the winter food of walrus, nor on seasonal food variations. Our knowledge is limited to a list of animals retrieved from the stomach of walrus in the summer months.



Fig. 17. A group of walrus on an ice floe. Chukchi Sea (photograph by V.M. Bel'kovich).



Fig. 18. Adult females and young walrus (left). Chukchi Sea (photograph by V.I. Krylov).

In the first two years juveniles survive on the mother's milk and take to independent feeding only in the third year. By then, the tusks have grown sufficiently large to enable the walrus to independently scrape food from the bottom of the sea. The main food items of adults comprise bottom-dwelling invertebrates (Table 1).

Throughout its extensive range, the walrus primarily feeds on various mollusks, which in the species composition of its food occupy first place. These are followed by crustaceans, of almost equal dietary importance. All the other food items, i.e., worms, echinoderms, ascidians, and fish, can be regarded as secondary. In the stomach of an Atlantic walrus, over a hundred polar cod were found (Chapskii, 1936); fish remnants were few in the stomach of Pacific walrus (V.I. Krylov); only remnants resembling otoliths were found in the stomach of walrus in the Canadian archipelago (Mansfield, 1958). In addition to the food items listed, the stomach of one walrus (site of find not mentioned) contained *Tridacna* (Moor, 1952*). Remnants of pinnipeds and even whales were found in the stomach of some walrus in all the regions studied.

The walrus seeks its food from the sea floor. It is assumed that it digs the bottom with its tusks, selects mollusks, breaks the shells, and eats the molluskan bodies. However, there is a suggestion (Mansfield, 1959) that the walrus bites only the soft, protruding portion of the mollusk, based on the fact that shells are very rare even in the stomach of those walrus caught immediately after feeding.

Table 1. Food of walruses in various regions

Atlantic walrus		Laptev Sea walrus (L.A. Popov, 1958 and 1959)	Pacific walrus (V.A. Arsen'ev, 1928; Nikulin, 1941; V.I. Krylov)
Kara Sea (Chapskii, 1936)	Canadian archipelago (Mansfield, 1958)		
Mollusks	Mollusks	Mollusks	Mollusks
<i>Mya</i>	<i>Mya truncata</i>	<i>Mya</i>	<i>Mya truncata</i>
<i>Buccinum</i>	<i>Saxicava arctica</i>	<i>Ioldia hyperborea</i>	<i>Saxicava arctica</i>
<i>Saxicava arctica</i>	<i>Astarte borealis</i>	<i>Buccinum</i>	<i>Saxicava rugosa</i>
<i>Cardium</i>	<i>Cardium</i> spp.	<i>Neptunia</i>	<i>Astarte borealis</i>
<i>Natica</i>	<i>Pecten</i> sp.	<i>Saxicava arctica</i>	<i>Ioldia hyperborea</i>
<i>Sclerocrangon</i>	<i>Buccinum</i> sp.	Crustaceans	<i>Macoma calcaria</i>
	<i>Natica</i> sp.	<i>Gammaracanthus</i>	<i>Serripes</i>
		<i>loricatus</i>	<i>groenlandicus</i>
<i>Hyas</i>	<i>Sipho</i> sp.	Worms	<i>Nucula tenuis</i>
<i>Isopoda (Mesidothea)</i>	Pelecypoda	<i>Echiurus</i>	<i>Natica clausa</i>
<i>Gammaridae</i>	Gastropoda	<i>Priapulius caudatus</i>	<i>Thyasira flexuosa</i>
Worms	Opercula		<i>Macra</i>
<i>Priapulius caudatus</i>	Squids (beaks)		<i>Astarte</i>
Echinoderms	Crustaceans		<i>Solariella</i>
<i>Cucumaria glacialis</i>	<i>Mesidothea sabini</i>		<i>Buccinum</i>
Fish	<i>Eupagurus kroyeri</i>		<i>Chrysodomus</i>
<i>Boreogadus saida</i>	<i>Sclerocrangon</i> sp.		Trochidae
			(<i>Margarites</i>)
	<i>Spirontocaris</i> sp.		<i>Polypus</i>
	<i>Eualis</i> sp.		<i>Octopus</i>
			<i>californicus</i>
	Decapoda		
	Paguridae		
			Fish
			Blennidae

Contd.

Table 1 Continued

Atlantic walrus		
Kara Sea (Chapskii, 1936)	Canadian archipelago (Mansfield, 1958)	Laptev Sea walrus (L.A. Popov, 1958 and 1959)
		(V.A. Arsen'ev, 1928; Nikulin, 1941; V.I. Krylov)
	Hippolytidae	
	Isopoda	
	Worms	
	<i>Priapulus caudatus</i>	
	Polychaeta	
	Echinoderms	
	<i>Cucumaria</i> sp.	
	<i>Thyonidium</i> sp.	
	Holothuroidea	
	Asciacea, otoliths of fish	
		Lumpenidae

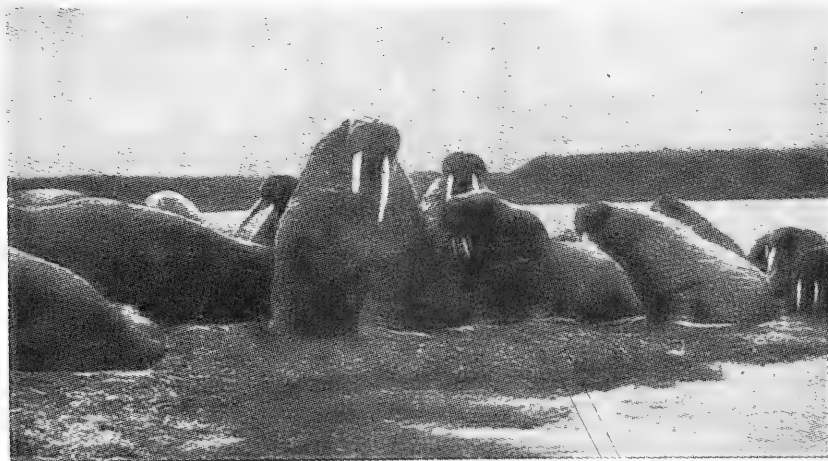
The walrus gathers food where it can easily reach, mainly at depths of 30 to 50 m (Nikulín, 1941). The depth to which the walrus dives while feeding can be as much as 180 m (Mansfield, 1959).

- 37 Some walrusés prey on seals and, occasionally, on birds. Seals usually avoid the area inhabited by a walrus-predator, but will return there if the predator is killed (V.A. Arsen'ev, 1935). Two categories of predatory walrusés are known: the first group feeds on uncommon foods occasionally when invertebrates are not available for some reason, while the second category comprises regular predators. The latter have long, thin, sharp-tipped tusks; these are lone males (Fay, 1955*).

Home range. There are no separate sections for individual walrusés or even for groups of them. In the absence of ice in summer, walrusés form coastal rookeries; however, it is still not clear whether the same animals return to the same sections. At the rookeries in the Laptev Sea, the same walrusés evidently return to their own sections (L.A. Popov, 1958).

- 38 *Daily activity and behavior.* No systematic diurnal activity has been established among walrusés.

The Atlantic walrusés of all ages and sexes gather on the beaches in August and September since there are almost no ice floes in the USSR waters in the regions of their summer habitat. There they remain, sometimes for 1.5 months, often going into the sea to feed. The animals driven away from the shore by stormy waves return to the beach as soon as the weather clears.



37 Fig. 19. A male walrus with a broken tusk. Chukchi Peninsula (photograph by V.I. Krylov).

The Laptev walruscs also form mixed coastal rookeries in which females with pups (Fig. 20) and juveniles live along with the large males. They lie in a definite sequence—females with pups close to the water, juveniles and the remaining adults farther away. They rest crowded together compactly in various postures, but mostly on the side. Yearlings and juveniles sometimes lie atop the adults. Fights are quite common between large bulls, who put their powerful tusks to good use. At all times, some animals are moving toward the water while some are returning to the rookery; thus the rookery is never quiescent (L.A. Popov, 1958). In September and October, the coastal herds disperse and the coast remains empty until the next season.

The Pacific walruscs spend much of their time on ice floes. Two types of colonies are distinguishable. One consists exclusively of adult males and the other of females with pups, among which a small number of males are sometimes observed. In calm weather walruscs sleep soundly. The resting animal does not even deign to look at a ship approaching the ice floe and, when disturbed, takes to water rather reluctantly. Walrus herds have often been observed resting on ice floes within 100 m of freshly killed animals. They did not react even to gunshots, the clatter
 39 of operating winches on a ship, nor to any other noise. Yet, in general, their hearing is better than their sight.

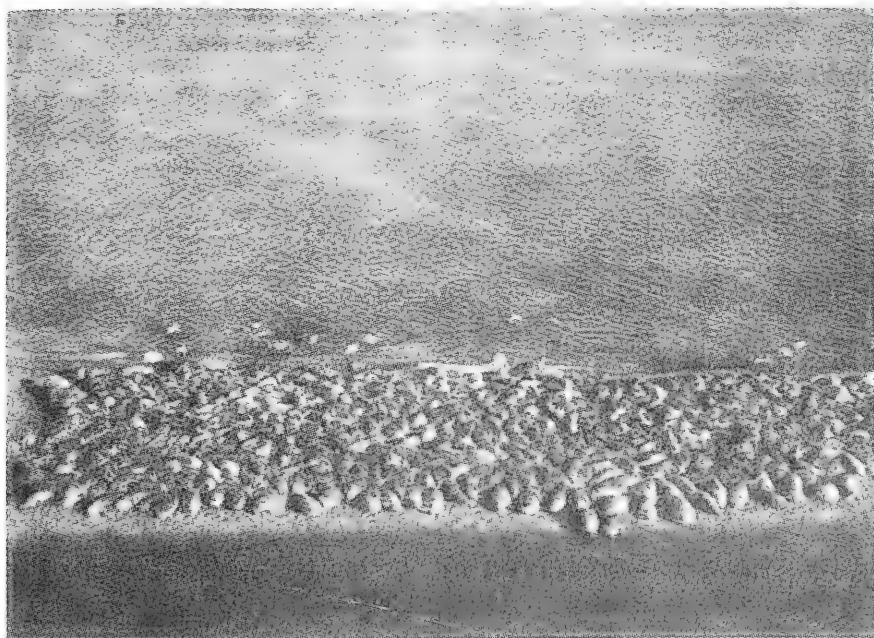


37 Fig. 20. Suckling walrus pup on an ice floe. Chukchi Sea (photograph by V.I. Krylov).

Exclusively male haunts are usually small but mixed herds run into several hundreds. The rookeries are mostly organized along the edges of drifting ice floes. The animals rest on permanent floes, whether smooth or hummocky. Frightened animals literally dive into the water, but soon surface, gather in herds, and begin groaning loudly. The herding instinct is strong among walruses (Dunbar, 1955). An injured animal is helped by others to float on the water surface. Pups that tire of swimming, often climb atop their mothers or any other walrus.

In autumn the Pacific walruses form coastal rookeries in some other regions as well (Fig. 21); these may be permanent or temporary. The latter can be classified as regular or occasional.

Only two permanent rookeries are preserved at present: at Rudder and Meechken in the Gulf of Anadyr. Only males, mainly 7 to 11 years of age, gather here (Fig. 21). Juveniles (mainly 4-6 years old) and older males come to the beach in small numbers. Females of all ages remain confined to ice floes during autumn. A few thousand walruses gather in each rookery, lie packed close together, often in two tiers. The more mobile young walruses, lying closer to the water, leave the shore more



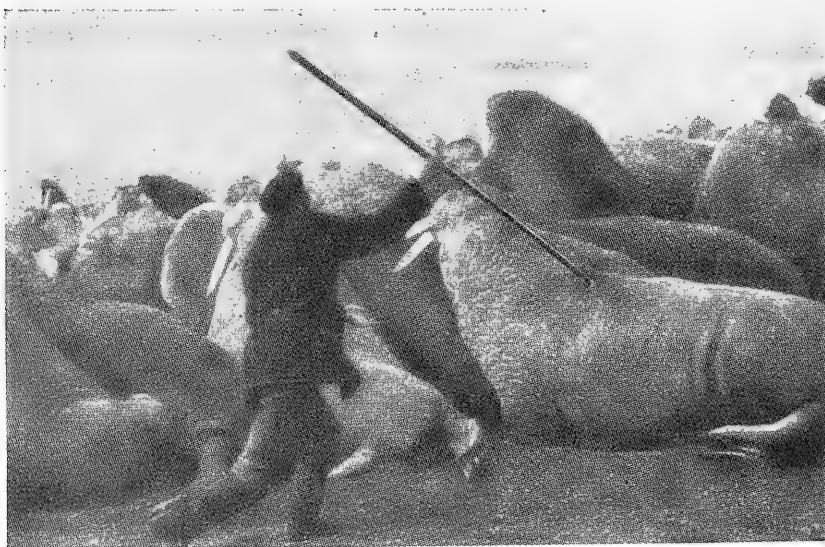
38 Fig. 21. Coastal rookery of male walruses. Chukchi Peninsula (photograph by P.G. Nikulin).

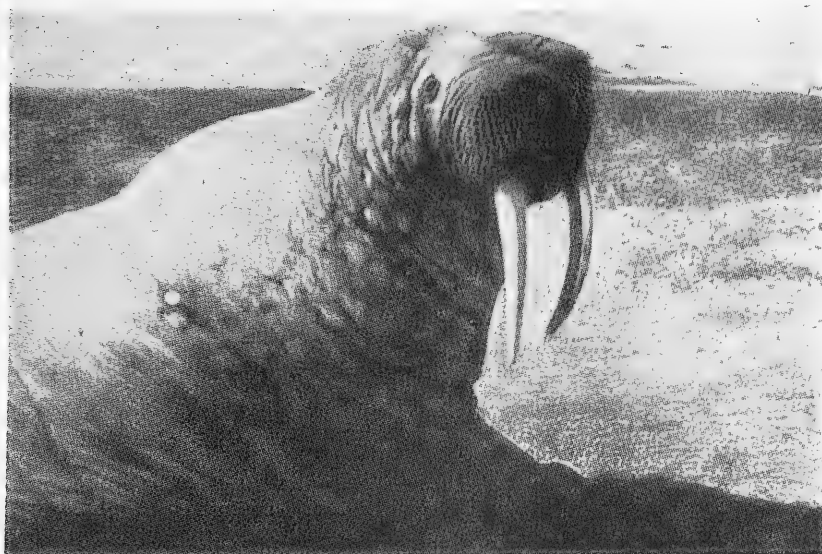
often than the older males resting farther away; then the older walrus become less densely crowded and rest for longer intervals and more peacefully. Permanent rookeries are formed at the end of August and function until the end of September-October when, with the appearance of ice floes, the walrus depart for them. During the period of walrus abundance on the Chukchi Peninsula there were many permanent rookeries, but now almost all of them are deserted.

Temporary rookeries serve as resting sites for walrus migrating from the Chukchi Sea to the Bering Sea. Such rookeries are visited by animals of both sexes and of all ages, including females with pups. The period of their formation and the population of animals depend on the ice conditions each year. Sometimes temporary rookeries contain 1,000 or more walrus, but animals may leave within 2-3 to 7-10 days.

- 40 Regular temporary rookeries are formed every year at the same places. Some 15 such were counted in recent years on Arakamchechen Island, in the region of villages Dezhnev and Ue'len, on Capes Intsov and Serdtse-Kamen', on Ildidlya and Kolyuchin islands, at village Vankarem on Karpkarpka island, and a few on Wrangel and other islands.

Finally, occasional rookeries are formed in the warm, less snowy years at the most unexpected places (sometimes even in villages). Walrus, tired of long sojourns in the water, form such rookeries, which





40 Fig. 23. Marked male walrus. Chukchi Peninsula (photograph by V.I. Krylov).

are extremely short in duration. Having rested on the coast, the animals quickly return to the sea, continuing their migration.

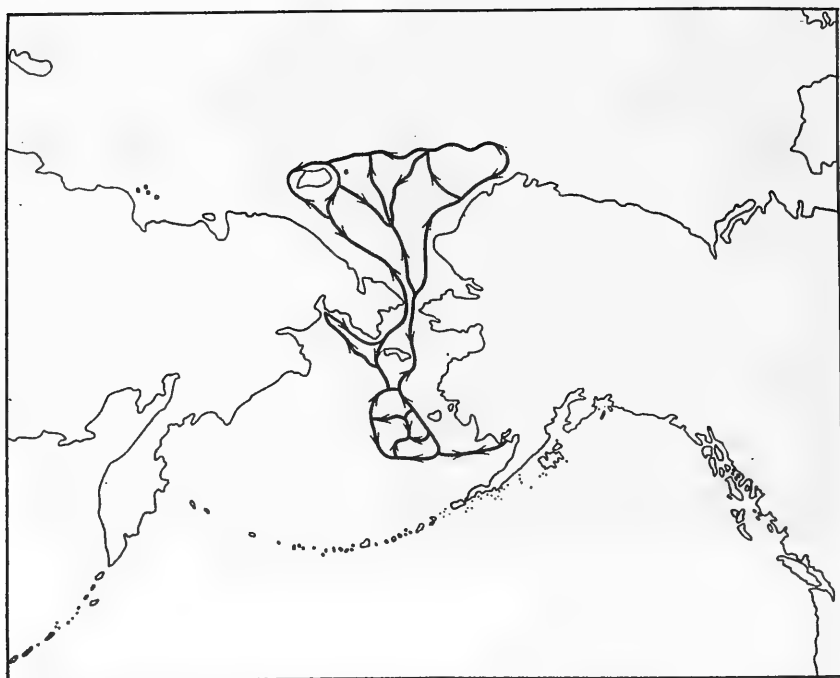
On the coasts of the Chukchi and Bering seas, over 30 permanent or temporary rookeries have been recorded in various years. At present, 15 have completely vanished, with no walrus recorded in them in recent decades (Gol'tsev, 1968).⁹

Walruses have often been observed sleeping on the water. Having filled its air sacs, the animal assumes a vertical posture with its head and the blown-up sacs of the neck jutting out of the water, and sleeps in that position (Nikulin, 1941).

Seasonal migrations and transgressions. Walruses perform regular seasonal migrations (Fig. 24) but the details of such migrations are not very clear.

The Atlantic walruses inhabiting our waters spend the winter-spring months in the southeastern part of the Barents Sea. In October, in the Kara Strait region, coastal rookeries are formed, but with formation of

⁹ In 1963, 500 Pacific walruses were marked for the first time in the Rudder rookery using a specially designed tag shaped like a large button with a base diameter of 3 cm and stem length of 5 cm. The tag was attached to a long pole and then jabbed into the skin of the walrus (Krylov, 1965). The animals permitted the markers to approach within the requisite distance (Krylov, 1965). No tags have been returned thus far (1967).



41 Fig. 24. Migrations of the Pacific walrus, *Odobenus rosmarus divergens* (V.A. Arsen'ev).

the ice cover, the animals return to the ice. In June, as the ice floes begin to drift, the walruses usually abandon this region and enter the Kara Sea by two routes: through the Kara Strait or by encircling Novaya Zemlya from the north.

- 41 The animals passing through the Kara Strait in the second half of July and in August inhabit the ice along the western coast of Yamal Peninsula from Belyi Island to Sharapov Spit. The easterly winds of August drive the ice away from here and the walruses migrate with it. By early October these animals are seen on the southern coasts of Novaya Zemlya close to the Kara Inlet, where they form coastal rookeries that function until formation of the ice cover.

Another group of walruses, together with the ice floes, migrates to the northern extremity of Novaya Zemlya and spends July-August on ice floes in the coastal waters. By September, as the drifting ice moves away from the Novaya Zemlya coasts, the animals begin to congregate in the immediate proximity of the coasts, mostly on the northeastern extremity of the island, and to form beach rookeries in a section from the Oransk Islands to Cape Sporyi Navolok. By October, ice has usually

begun to form afresh on the northern coasts of Novaya Zemlya and the walrus abandon the coastal waters and move onto the drifting ice to reach the Barents Sea. They move along the western coasts of Novaya Zemlya and by the end of the month have reached their winter habitat in the southeastern part of the Barents Sea (Chapskii, 1936).

The migrations of the Laptev walrus have not been studied. In August-September they form coastal rookeries, mainly on the southwestern strip of the sea, on Faddei, Andrei, Preobrazhen'e, Begichev, the Peschan Islands, and in Pronchishcheva Bay. In the autumn, as the ice floes appear, the walrus move onto them and migrate northward, spending the winter in ponds of open water in the ice and in cracks fairly
42 close to the coastal rookeries. In August, 1951, some 400 walrus were sighted at 87° N lat. and 140° E long. (Uspenskii, 1958), which perhaps could be regarded as having strayed beyond the range.

The Pacific walrus spend the winter in the shallow waters of the southeastern part of the Bering Sea, reaching the area of compact ice floes in Bristol Bay. In March-April, they begin moving northward on the ice floes, approaching the coasts of Chukchi Peninsula in the Provideniya Bay-Cape Chaplin region. In May, walrus are seen even in the Bering Strait, and by June have emerged, together with the floes, into the Chukchi Sea, reaching Wrangel Island. During July, however, walrus herds continue to move through the Bering Strait and spread out in their summer grounds, from the eastern part of the East Siberian Sea to Point Barrow in Alaska, only in August.

In mid-October, when intense formation of new ice occurs and polar ice starts to drift southward, the walrus move to the Chukchi coasts. They swim mostly through clear waters for a distance of 50 - 100 km from the coasts to the Bering Strait and, entering the Bering Sea, proceed to their winter grounds. Large walrus herds swimming to the Bering Strait, even among compact ice floes, have been sighted in October, evidently struggling to escape the fast-freezing sea (P.G. Nikulin).

Some walrus remain in the Gulf of Anadyr in summer on the ice floes of Cape Bering and Krest Bay until the ice has completely cleared, after which they remain in clear water. In July-August, coastal rookeries are formed in the Gulf of Anadyr (Rudder) and, at this time, some walrus move in groups or singly in the clear water along the Chukchi coasts eastward, forming new rookeries in the Bering Strait (Arakamchechen) and even at its confluence with the Chukchi Sea (Inchoun). They remain there until the end of September or October, after which the animals move onto the ice. Rookeries are also found on Wrangel and Herald islands (Belopol'skii, 1939; Nikulin, 1941; Kleinenberg *et al.*, 1964).

Walrus finds outside their usual range have been reported for both the Atlantic and Pacific populations. Almost every year single walruses are sighted in summer and autumn in the inlet of the White Sea and in Mezensk Bay. In 1956, a walrus was killed on the eastern Murman coast (Bel'kovich and Khuzin, 1960). Walruses have been sighted on the coasts of Norway, mainly in the northern areas. A walrus was found in 1902 and 1903 in G'esver Fjord, in 1904 close to Trondheim, in 1917 around Kirkenes, and in 1931 in Grosbaken Fjord. Two walruses were sighted in 1942 at Finmarken, and in 1953 one was found lying on the beach at Makkaur lighthouse (Lund, 1954).

An interesting journey of a walrus along the Norwegian coasts has been described. In October, 1926, in the southern part of Norway (Haugesund), a male supposedly from the coasts of Scotland was sighted. The same male was seen on November 11 on the coast of Holland, at the end of November on the northern coast of Denmark (near Skaagen), and finally on January 9, 1927, was killed in Bokhuslan region in Sweden. An even more amazing journey was performed by another male in 1954 (assuming that it was the same animal throughout). In early January, a male was noticed at the northernmost tip of Norway in Bakkeby region and then sighted on Trena Island on February 3, having traveled 600 km in 26 days. From there, the walrus took to the coast on March 15 and traveled another 700 km south into Batalden region, from where it entered Swedish waters. It soon returned northward and, on March 27, beached around Sul (about 62° N lat.), then traveled still northward. In mid-April, it was sighted on Helligwer Islands (67° N lat.), again near Trena, and then at Lofoten. In mid-June, the male was seen at 69° N lat. at Sandesundver (Lund, 1954).

The following journeys of Pacific walruses are known. In 1931, a herd was sighted in Korf Bay (60° N lat.) in Kamchatka, in the summer of 1935 about 500 of them inhabited Natalii Gulf (61° N lat.), in 1939 they were sighted on Karaginsk Island (59° N lat.) and on Cape Paklan (59° 40' N lat.), and in August of the same year they surfaced on the coast of Verkhoturov Island (59° N lat.) where two of them were killed. In July, 1969, 20-25 walruses were sighted. Some walrus skulls were found on the Commander Islands while in the summer of 1969 three carcasses were found. One of them, a female 3 m long with 60 cm long tusks, found on June 17, was torn to shreds by polar foxes (some 40 of them gathered), which lends credence to this animal having been killed on the coast (Chugunkov, 1970) (Fig. 25).

In May, 1940, close to Yamsk Islands (northeastern part of the Sea of Okhotsk), not far from a rookery of fur seals, a young female was killed (without embryo, length of tusks 20 cm) (Moiseev, 1951).



43 Fig. 25. The carcass of a female walrus found on the coast of Mednyi Island. A polar fox is seen on the carcass (photograph by D.I. Chugunkov, 1969).

Possibly, this was one of the pups which hunters often took onboard ship in the Chukchi Sea. However, in the summer of 1966, on Yamsk Islands, four adults were again seen (G.A. Fedoseev). In April, 1954, a large female was killed on Kad'yak Island in the Gulf of Alaska (Fay, 1957).

Reproduction. Information on walrus biology is predominantly collected in the summer months during the hunting season and hence data on breeding are extremely scant. Data on the Pacific walrus are somewhat more comprehensive.

The growth of follicles in the ovaries commences in the first half of April and mature follicles are seen in early May; such follicles are present in gestating females as well. In the first half of June, the growth of follicles ceases. In mid-May, ruptured follicles are replaced by corpora lutea, indicating the fertilization of egg cells.

Mature spermatozoa form in males in early April; by the first ten days of June spermatogenesis has ceased. The maximum quantity of mature sperm is observed from mid-April to May end. Thus the mating of walruses occurs during May and to a lesser extent in early June. By this time, some females are already with embryos in the early stages of growth (Fig. 26).



44 Fig. 26. Embryo of the Pacific walrus, *Odobenus rosmarus divergens*. Bering Sea (photograph by V.I. Krylov).

44 Pups are born in about the same period as mating—from April end to May end. Individual instances of birth are known in early June as well. The period of whelping extends for a month or more. Hence gestation extends for almost 12 months. Whelping duration can be ascertained from the differences in the sizes of embryos found at a given time. Thus the length of embryos investigated on July 30 varied from 13 to 21 cm, on August 30 from 27 to 37 cm, on September 14 from 34 to 47 cm, and on September 23 from 43 to 53 cm.

The embryos of Pacific walruses measured in the same period were 5-11 cm longer than those of Atlantic walruses and 4-7 cm longer than those of the Laptev Sea. This suggests either a very early whelping in the Pacific walrus, or that the much larger size of this subspecies is determined even during embryonal growth (Krylov, 1966, 1969).

The reproduction tempo of walruses is the slowest among all the species of pinnipeds and the whelping pattern is highly complex. Among the Pacific walrus females (285 studied) mothers were seen suckling pups born in that year and again gestating; suckling yearlings and gestating; and some gestating but not lactating; i.e., females at different stages of reproduction were encountered. The following relationships have been established between groups of females with different reproduction rhythms (Krylov, 1968):

Females, whelping annually	4.5%
Females, whelping once in two years	12.3%
Females, whelping once in three years	42.2%
Females, whelping once in four years	41.0%

The reproduction rhythm of Laptev walruses is similar to this pattern (L.A. Popov, 1960).

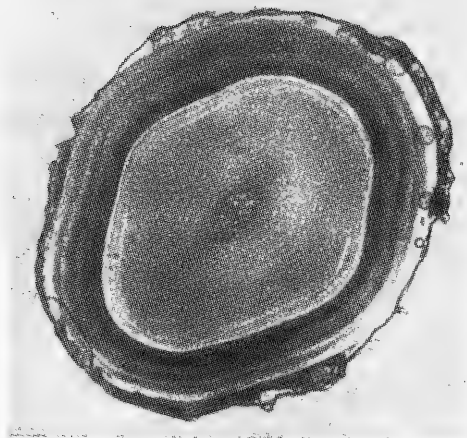
Young females have a more frequent reproduction rhythm compared to older ones. Most females with an annual whelping cycle fall in the age group 6 to 11 years; those with a three-year cycle from 12 to 18 years; and those whelping once in four years or more are over 15 years of age (Krylov, 1968). The annual population growth is 8% since the average of pups per mature female is 0.35 (Mansfield, 1959).
 45 According to other data, the annual population growth is 11.2% (Krylov, 1968).

The prevailing view regarding polygamy among walruses (Allen, 1880; Nikulin, 1941; Freiman, 1941) has not been confirmed by recent investigations. During the period of reproduction walruses do not form harems but live in family groups of three to six animals comprising the male, female, and pups of different ages (Tikhomirov, 1964c; Krylov, 1968). Ice is not a suitable substratum for organizing a harem, whether of walruses or other pinnipeds (N. Smirnov, 1937*).

Growth, development, and molt. Reliable information on the growth of walruses (and other pinnipeds) became available only after the development of a method for determining the age of each animal. Age is determined from the annual depositions (rings) in the dentine of the teeth (Fig. 27). This method has been verified in many species of marine and land animals and is generally accepted (Tikhomirov and Klevezal', 1964*).

Differences in the tempo of growth of males and females are perceptible already in the juvenile and persist throughout their lives (Table 2).

Pups of both sexes grow very fast. The tempo of growth slows down
 46 at two years of age, evidently due to a changeover from suckling to independent feeding. Again, a reduced tempo is seen in females of 7-9 years and males of 8-9 years. This lag coincides with the period of sexual maturity, which in females begins at 6-8 years with the peak in the 7th year, and in males at 7-9 years with the peak in the 8th year. This is followed by a fairly uniform increase in body length in females up to 11-14 years and in males up to 17-20 years. Very slow growth continues up to 20 years in females and up to 23 years in males; thereafter body growth ceases. Females older than 25 years enter a climacteric period and old males also evince no interest in mating. Among females whose



45 Fig. 27. Annual layers on a polished section of a cheek tooth of the Pacific walrus, *Odobenus rosmarus divergens* (photograph by V.I. Krylov).

age was determined, the oldest was 30 years, and among males 43 years (Krylov, 1966, 1967, 1968).

The body growth curve of walruses of the Canadian archipelago is very similar. Here, by the beginning of the third year, the body length of walruses averages 2 m and weight 340 kg; the average length of adult females is 2.6 m and weight about 505 kg; the corresponding values for males are 3 m and 750 kg. The maximum weight of females is 725 kg and of males 1,270 kg. Females cease to grow in the 15th and males in the 20th year (Mansfield, 1959).

Simultaneous with increasing body length the tusks grow in length and thickness. The newborn pup has no teeth and the canines begin to cut a few months later. By the end of the first year, the canine measures 2.6 cm (average of five measurements; V.I. Krylov) or 2-9 cm (Mansfield, 1959). Slowing down of the tempo of tusk growth is commensurate with that of body length. Tusks grow throughout the animal's life but detecting their growth in adults is impossible because they wear down constantly, thus decreasing in length. The tips of male tusks diverge sideways, while those of females are slightly proximate. This difference is distinctly visible in the frontal view. Female tusks are thinner and somewhat crescent-shaped, while those of the male are stronger and almost straight.

The sex ratio in newborns is close to 1:1. Suckling extends for about two years but the stomach of pups older than a year often contains mollusks along with milk; the stomach of those older than two years

Table 2. Change of body length with age in the pacific walrus (V.I. Krylov)

Age	Male		Female	
	No. of animals	Mean length	No. of animals	Mean length
Newborn	4	138	8	129
1 - 4 months	3	158	5	146
Year-old	5	198	11	185
2 years	4	238	5	218
3 years	6	247	3	238
4 years	7	260	7	258
5 years	11	281	11	268
6 years	13	292	6	276
7 years	24	297	7	276
8 years	25	306	6	278
9 years	30	306	11	286
10 years	49	322	13	290
11 years	32	337	8	307
12 years	45	338	18	308
13 years	24	338	8	298
14 years	30	352	17	307
15 years	35	354	25	299
16 years	43	351	18	308
17 years	34	358	22	304
18 years	35	358	15	312
19 years	31	362	8	315
20 years	29	370	10	311
21 years	19	371	8	312
22 years	12	370	4	328
23 years	17	375	7	326
24 years	14	371	8	321
25 years	14	369	4	321
26 years	13	372	4	321
27 years	4	367		
28 years	12	370		
29 years	7	371		
30 years	12	363		
31 - 32 years	6	370		
33 years	5	372		
34 - 38 years	7	374		

sometimes contains milk. Females under parturition every year suckle two pups simultaneously—the newborn and the yearling.

The first molt occurs soon after birth. In the first few days the body of the pup is covered rather densely with grayish-brown hairs, which are gradually shed and become sparse 1-2 months later. Adults have large bald patches and the hairs are small and sparse in other places; however,

they molt every year. The period and duration of molt have not been established but evidently molt extends over a few months. In July and August, most of the walrus studied in the Bering and Chukchi seas had hairs that could easily be pulled out, while some animals had already grown strong new hairs by early July (Nikulin, 1941). In the Kara Sea in July to October, hairs of "various stiffness" were observed (Chapskii, 1936).

Enemies, diseases, parasites, mortality, and competitors. The enemies of walrus are killer whales at sea and polar bears on ice (rarely also in coastal rookeries). The killer whale more often attacks the young, smaller animals but can be dangerous even to a large animal. In 1936, in the Gulf of Anadyr, whales attacked a herd of walrus under observation. Some 15 killer whales encircled a group of 60-70 walrus. Two whales broke into the center of the herd, split it into groups of 10-12 animals, and totally destroyed one such group. Meanwhile, the rest of the walrus in the compact group rapidly swam to the coast. The stomach of a killer whale caught on August 11, 1936 in the Gulf of Anadyr revealed the skin, blubber, and pieces of flesh of a walrus (Zenkovich, 1938). Only a large male can keep the polar bear at bay; however, this predator is not a significant threat to walrus herds.

The only species of lice known among the ectoparasites of walrus, 47 *Antarctophthirus* Boh., is found in large numbers in the whiskers, in the skin folds on the sides, in the hind flippers, around the anal opening, etc. Up to 10 lice per cm² of skin were counted here and there (Ass, 1934).

Eleven species of endoparasites are known. The trematode *Ohdneriella rossica* Skrjabin, parasitizing the hepatic ducts of the liver, has been reported only in the walrus. *Orthosplanchnus fraterculus* Odhner, a parasite of the gall bladder, has been found in the walrus, the bearded seal, and the sea otter. The cestode *Diphyllobothrium cordatum* Leuckart, which inhabits the small intestine of the walrus, has also been found in the bearded, common, and Greenland seals; *Diphyllobothrium latum* has been reported in many species of pinnipeds and whales, in land carnivores, and in man. *Diphyllobothrium romeri* Zschokke has been found in the small intestine of only the walrus. The nematode *Anisakis* (*Anisakis*) *rosmaryi* Baylis is found only in the walrus stomach. *Contracaecum osculatum osculatum* Mosgovoy and Ryjikov localizes in the stomach and small intestine and is found in many species of pinnipeds of the Northern and Southern hemispheres. *Terranova* (*Terranova*) *decepiens* Krabbe, parasitizing the stomach and intestine, has a wide range of hosts among pinnipeds and cetaceans. Three species of acanthocephalans parasitize the intestine. *Corynosoma strumosum* Rudolphi has been found in seven species of pinnipeds and two species of cetaceans; *Corynosoma semerme*

Forssell in three species of seals, in guinea pigs, and in many birds. The third species is *Corynosoma valdum* van Cleave.

Ten of the 11 known species of helminths of walruses have been reported in the Atlantic walrus, but only five in the Pacific walrus, perhaps due to the thoroughness with which helminths were studied in the former (Margolis, 1954; Delyamure, 1955).

The diseases and natural mortality of walruses have not been studied. It has been suggested that mortality may reach 18-20% of the annual population increment (Chapskii, 1936), which is rather doubtful. Probably, the mortality of pups during the first two years of life is extremely insignificant because of the two-year lactation cycle and the absence of a large number of enemies.

Adult mortality is mainly the result of hunting by man. Mortality, mainly of females and pups, occurs in coastal rookeries due to suffocation by much larger animals. On St. Lawrence Island, in 1936, a large herd of walruses was chased to the coast by killer whales and more than 20 of them were crushed as a consequence. In July, 1949, 54 dead walruses (mostly females) were found on Pujuk Island 5 km from St. Lawrence Island (Schiller, 1954).

In November, 1951, many walrus carcasses were found on the coast of St. Lawrence Island. All of them were greatly decomposed, their heads severed, and the limbs hanging from the skin. More than 50 carcasses lay on the beach and many more were afloat in the sea. Based on age and sex composition (as far as could be determined from such remnants), a whole herd had perished. The investigator felt that the animals had been killed by a massive wave (possibly caused by an underwater explosion) close to the Siberian coast, where they sank, then floated after decomposition, and were brought by winds and currents to the coast of St. Lawrence Island. The deaths were evidently not due to infection, as the Eskimos fed this meat to their sledge dogs and used it as bait for foxes (Schiller, 1954). The cause of mortality of this herd remains unestablished.

The bearded seal, which also feeds on benthic invertebrates, competes with the walrus for food to some extent, as mollusks and crustaceans are of great importance as food for this seal (Pikharev, 1941). There are no animals which compete with the walrus in habitat selection on the coast or on ice.

Population dynamics. The walrus population throughout its range has greatly decreased, mainly as a result of hunting. At present, in the Soviet Union, the USA, Canada, and Norway, hunting has been banned.

48 The inhabitants of the Chukchi Peninsula and Alaska are permitted to hunt walruses, however, to meet their personal requirements.

Information is not available on the population dynamics of walrus of the Atlantic Ocean and Laptev Sea. The population dynamics of the Pacific walrus is as follows: 1850-1860, 200,000; 1860-1880, 150,000; 1880-1910, 80,000; 1910-1950, 60,000; and 1950-1956, 45,000 (Fay, 1957). Some attempts have been made in recent years to determine the population by different methods: aerial photography, aerial observations, observations from sealing vessels and in coastal rookeries. The total walrus population in the waters of the USSR was roughly estimated at 30,000. Considering that approximately 20,000 walrus were counted in American waters during the summer months, the entire walrus population may be estimated at 50,000 (Zenkovich, 1938; Collins, 1940; Buckley, 1958; Fedoseev, 1962; Gol'tsev, 1968; Krylov, 1968).

Field characteristics. The walrus is a large animal with a huge thickset body, relatively small head, and broad blunt snout, with two huge tusks directed downward, which are absent in all other pinnipeds. These tusks are not visible in one-to-two-month-old pups, or they are so small as to be indistinguishable. The skin lies in large wrinkles and folds, and the hairs are sparse and coarse in adults.

Walrus form large herds on ice or beaches, on which they are densely packed (Fig. 28). The animals swimming in water present a characteristic picture of a round head with long tusks. (V.A.)

Economic Importance

Walrus hunting is not important to the overall economy of the country but is significant in the economy of some regions. In the Chukchi Peninsula, the walrus is one of the main sources of raw material for the local inhabitants. Products of walrus hunting have served as food for the people and sledge dogs, and material for building canoes and even houses ("yarangas") until quite recently. Shoes, dresses, harnesses for dogs, etc. are made from this raw material.

Walrus hunting is done by two methods—by boats (now banned) and on the coast. Sealing at sea was done from specially designed small wooden schooners. As the schooner approached a breeding site on the ice, motorized whaleboats were lowered from the sides and hunting commenced. Occasionally, walrus were shot directly from the schooner. Walrus were killed using firearms, for which reason crews of the hunting vessels always included some sharp shooters. The skin with the blubber was removed from the animals killed on the ice and the animals then hauled in parts onboard the schooner.

Sometimes walrus swimming in water are killed (this practice has been banned recently). In this method, a manual harpoon is hurled,

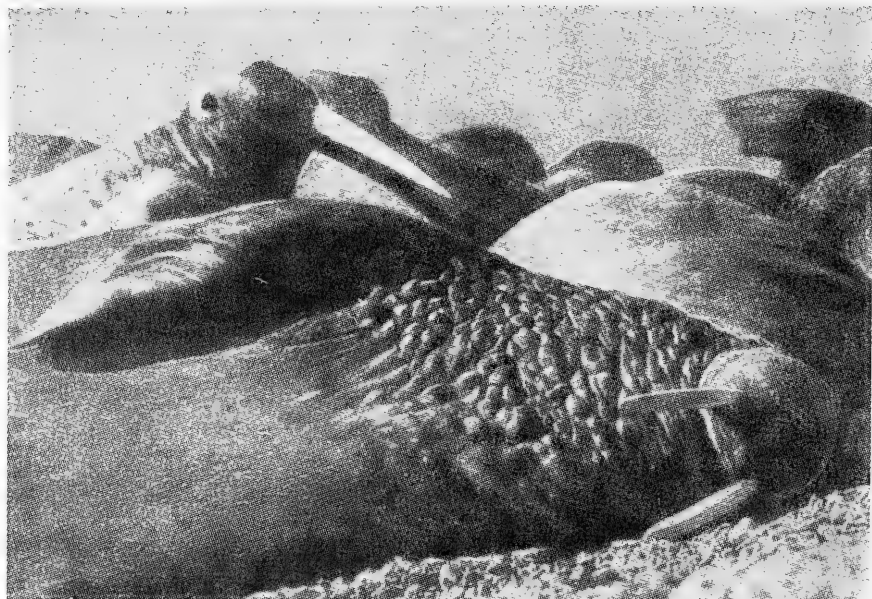


48 Fig. 28. A coastal rookery of walrus in the Gulf of Anadyr (photograph by A.V. Yablokov).

piercing the body of the priorly injured or killed animal. The harpoon is connected by a short line to floats (inflated seal skin or various types of artificial floats) which prevent the carcass from sinking. Hunting in water has invariably been wasteful because no less than 40% of the killed animals sink and are lost (P.C. Nikulin and V.I. Krylov). According to Canadian investigators, such losses have been no less than one-third of the kill (Mansfield, 1959).

When hunting from a ship, the hide with a layer of blubber is prepared and salted in the hold and brought to the processing plant on the coast. The carcass is sometimes brought to the coast and given to the locals but quite often simply left behind. Only recently has the bringing of the carcass to the coast been made compulsory. In all methods of hunting the tusks are invariably removed and used in the making of various articles.

Local hunters use rifles in hunting walrus in their breeding sites on ice floes. The sea is surveyed constantly from high ground and when walrus drifting on floes are sighted, the hunters enter the sea. Hunting is done by a team of 7-10 men from motorized whaleboats or indigenous canoes (now rare) fitted with outboard motors. The whaleboat approaches the floes as closely as possible and then the hunters open



50 Fig. 29. "Warts" on the skin of an adult male. Chukchi Peninsula (photograph by A.V. Yablokov).

fire. The body of killed animals is cut into large pieces, which are stacked in the whaleboat and brought to the coast. Wounded walruses are harpooned and then shot.

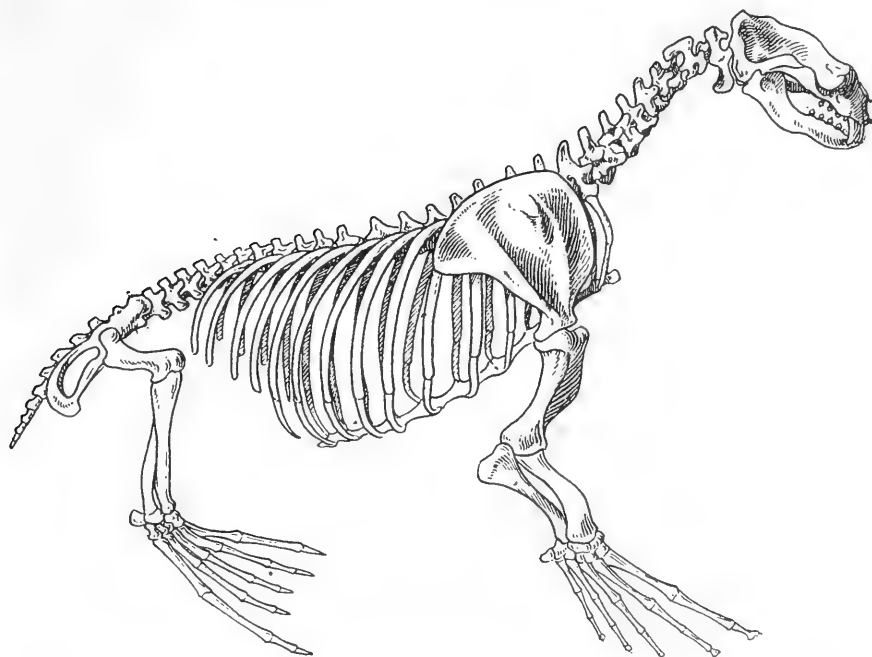
Hunting in coastal rookeries is of little significance. It is resorted to only by the locals for whom some areas are reserved. Killing is done using special pikes mounted on long poles. No sound is permitted. Hunters follow a strict sequence of killing, conforming to traditional practices geared to conservation. Only some and not all the walruses are killed. It is believed that a colony ceases to exist if all the walruses present in it are killed. Campfires and other types of contamination of the rookeries are prohibited as such scare the animals. The tradition prohibiting the killing of all animals is based on the assumption that the same walruses return to the same region year after year.

The number of coastal rookeries in the Chukchi Peninsula and their populations have decreased considerably. If at the beginning of the 1930s there were more than ten permanent rookeries, only two are known at present. Thus walrus hunting in the coastal rookeries has lost its earlier importance. At present, walrus hunting is done in summer when herds

50

Table 3. Walrus hunting in the Chukchi Peninsula (Krylov, 1968)

Year	Total killed	Of which	
		Used	Losses (40%)
1932	5,180	3,750	1,480
1935	9,730	6,950	2,780
1938	11,570	8,264	3,306
1941	5,043	3,602	1,441
1944	4,654	3,324	1,330
1947	4,410	3,150	1,260
1950	5,642	4,030	1,612
1953	3,815	2,725	1,090
1956	8,140	5,814	2,326
1959	4,456	3,183	1,273
1961	3,602	2,573	1,029



51

Fig. 30. Skeleton of an eared seal (Steller's sea lion) (figure by N.N. Kondakov).

migrate on ice floes close to the coasts or in regions of their summer habitat on ice floes.

50

During this same period, in Alaskan waters an average of 2,200 to 2,600 walrus were killed, of which some 1,300 were used (30-50% loss). Thus about 10,000 Pacific walrus were killed annually. Attempts

to shoot the much larger animals led to the preponderance of males in the catch which disturbed the natural sex ratio (Fay, 1957; Scott and Kenyon *et al.*, 1959; Krylov, 1968).

After the banning of state hunting, the catch of walruses in waters of the Chukchi Peninsula reduced: an average of 2,000 animals were hunted here until an annual limit was imposed, initially at 1,000 and later raised to 1,500.

The slow tempo of reproduction determines the extremely slow restoration of depleted herds of walruses. In order to conserve
51 their stocks, measures aimed at conservation of animals and hunting regulation are necessary. Primarily, restriction on hunting is necessary for each individual herd, so that the killing will not exceed the annual increase in population and, consequently, not deplete the stocks.

The prospects of exploiting the Pacific populations may be based on the following premises: total population 50,000; sexually mature, 70% of the herd; at a 1:1 sex ratio, mature females form 35% of the total population or 17,500. About 8.5% of the females do not take part in reproduction, i.e., only 16,000 females are productive. The pups born per annum number 5,600. Keeping in view not only the need for population conservation, but also the need to reinforce it steadily, the annual catch in Chukchi and Alaskan waters should not exceed half the annual population increment or 6% of the population, i.e., about 3,000. Further, measures should be taken to cut down the irretrievable hunting losses. (V.A.)

SUPERFAMILY OF EARED SEALS

Superfamily OTARIOIDEA Smirnov, 1908

Family of Eared Seals

Family OTARIIDAE Gill, 1866

Males are stocky and large animals while females are of moderate size with a lighter build. The head is elongated, narrowed exteriorly, and proportional to the body size. Small pinnae are present. The neck is long and movable.

The limbs are very long, the fore flippers usually are not shorter than
52 the hind ones and terminate in skin-cartilaginous tips; their undersurface is bare. Claws on the fore flippers are either absent or rudimentary. The hind flippers are capable of bending forward under the trunk and help in movement on land. The claws on the three middle digits of the hind flippers are small but well developed and disposed far from the outer margin. Claws are absent on the two extreme digits.

Color varies from black to straw-yellow in the various age and sex groups. The guard hairs on the neck of adult males are long and form a fairly perceptible short "mane". The adipose layer is insignificant.

The testes are in the scrotum.

There are four teats.

The width of the skull above the canines is $1/2 - 1/3$ that over the ear openings. The nasals are separated posteriorly by an acute projection of the frontals (Fig. 31). The supraorbital processes are well developed. The bony palate is relatively flat. The structure of the tympanic bullae is complex, flattened, and relatively small. Articular, mastoid, and paroccipital processes are fused into an extremely massive projection, jutting far downward and sideways beyond the margin of the tympanic bulla.

The teeth are well differentiated into incisors, canines, and molars. The upper and lower canines are roughly identical in size, with the upper ones normally developed (not transformed into large tusks), and the molars conical. The distinct milk teeth are well developed and are shed a few weeks after birth. The dental formula is:

$$I \frac{3}{2}, C \frac{1}{1}, P \frac{4}{4}, M \frac{2-1}{1} = 36 - 34.$$

The scapula is stunted but broad, the humerus and often the ulna is shortened, but the elements of the hand are extremely elongated and form a large flipper.

Sexual dimorphism is very pronounced, while age-related dimorphism is insignificant.

The family is characterized by distinct polygamy and large harems are formed in the summer rookeries. The animals survive mainly on certain

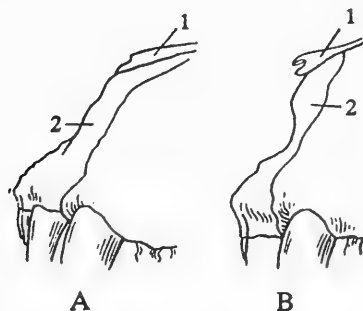


Fig. 31. Nasal portion of skull. A—Steller's sea lion, *Eumetopias jubatus*; B—northern fur seal, *Callorhinus ursinus* (figure by N.N. Kondakov). 1—nasal bone; 2—premaxillary bone.

types of fish and cephalopods. Eared seals undertake regular seasonal migrations.

These seals inhabit warm and temperate waters of the Northern and Southern hemispheres, entering cold seas only in the summer months. In the Northern hemisphere they inhabit only the Pacific Ocean and the surrounding seas; in the Southern hemisphere they live along the Pacific coast of South America and then along the coasts of Australia and New Zealand. They are found in the Atlantic Ocean along the coasts of South Africa and South America and also on many subantarctic islands. They are not found in the northern half of the Atlantic Ocean (Fig. 32).

The systematics of the family have not been properly worked out. Eared seals have sometimes been grouped into one family with the walrus and assigned the rank of a subfamily; at other times the two groups have been regarded as independent families. The majority of authors attribute a common origin to them.

This fact and the similarity of several vital morphological features justify combining the two families into a single superfamily, Otarioidea Smirnov, contrasting them jointly with the family of true seals, Phocidae, considered under the superfamily Phocoidea Smirnov. In general, however, within the order the family is regarded, quite justifiably, as the least specialized (primitive); some authors have compared their origin with that of the family of bears (Ursidae) of the order Carnivora.

- 54 The family comprises 13 genera, of which seven are extinct and six extant. Members of four of the extinct genera (*Allodesmus*, *Neotherium*, *Desmatophoca*, and *Pithanotaria*) first appeared in the Lower Miocene, the genus *Dusignatus* in the Upper Miocene, and the other two (*Pontolis* and *Pliopedia*) in the Middle and Upper Pliocene. All the fossils of Otariidae have been found on the Pacific coast of North America and for this reason this area may be considered the center of origin of the family (Simpson, 1945; Scheffer, 1958; Mitchell, 1966).

Among the extant genera, *Arctocephalus* is known from the Pliocene of South America and the Pleistocene of New Zealand, i.e., within the distribution range. Two other extant genera (*Zalophus* and *Eumetopias*) are known from the Pleistocene, also within their contemporary range.

The extant fauna includes 6 genera with 12 species: the genus of southern sea lion, *Otaria*, with one species, *O. byronia* [= *O. flavescence*]; the genus of Steller's sea lion, *Eumetopias*, with one species, *E. jubatus*; the genus of Californian sea lion, *Zalophus*, with one species, *Z. californianus* (with three subspecies); the genus of Tasmanian sea lion, *Neophoca*, with two species, *N. cinerea* (Australia) and *N. hookeri* [= *Phocarcos hookeri*] (New Zealand); the genus of southern fur seals, *Arctocephalus*, with six species: *A. pusillus* (South Africa), *forsteri*

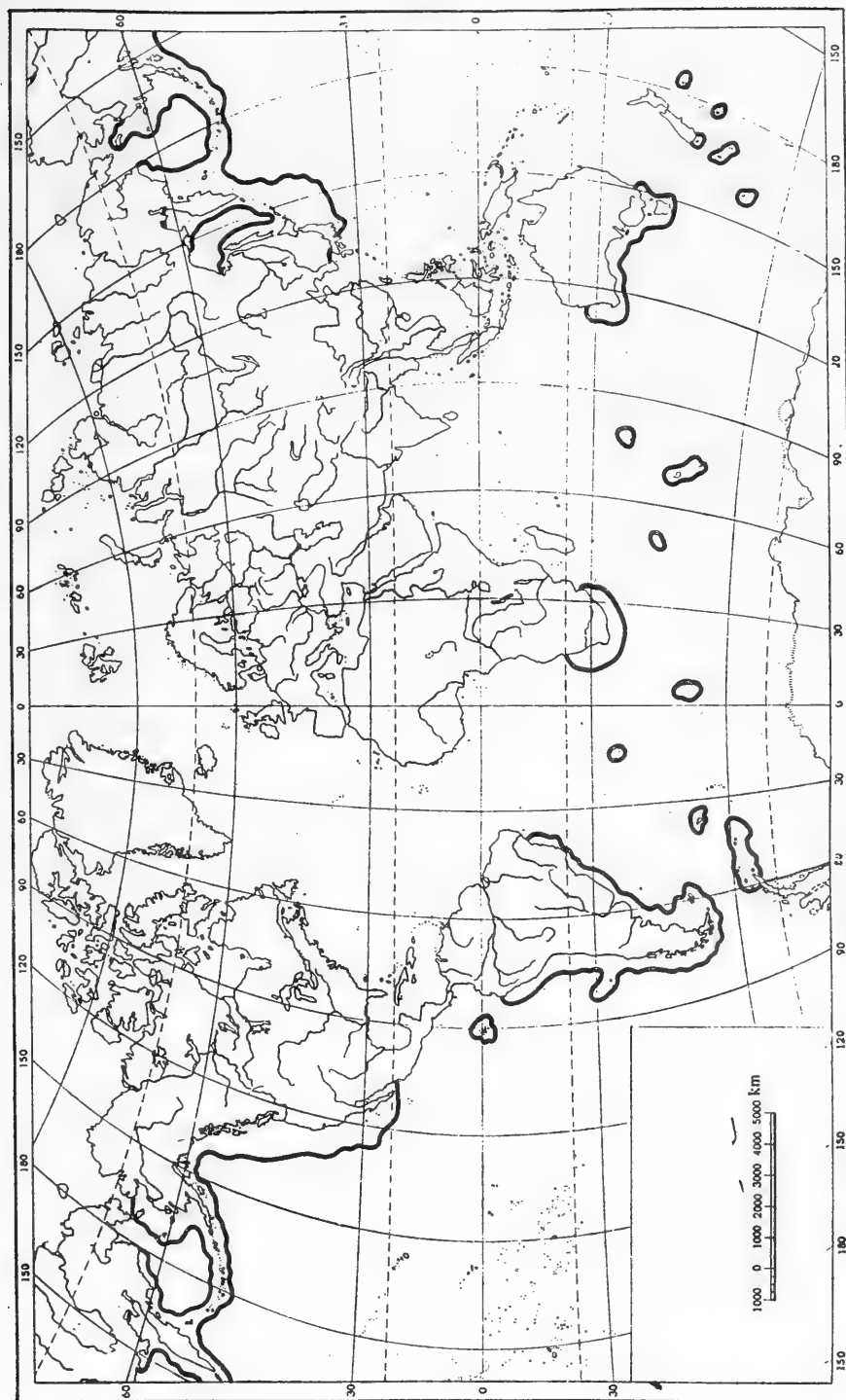


Fig. 32. Range of the family of eared seals, Otariidae (V.A. Arsen'ev).

(New Zealand), *doriferus* (Australia), *gazella* (Kerguelen), *australis* (South America; includes three subspecies), and *philippii* (possibly two subspecies) [most authors recognize three additional species of *Arctocephalus*: *townsendi* (Guadalupe Is.), *tropicalis* (subantarctic) and *galapagoensis* (Galapago Is.); and the genus of northern fur seals, *Callorhinus*, with one species, *C. ursinus* (with three subspecies).

Some authors (Scheffer, 1958; and others) are inclined to divide the extant family into two subfamilies: Otariinae Boetticher with the genera *Otaria*, *Eumetopias*, *Zalophus*, and *Neophoca*, and a more specialized Arctocephalinae Boetticher with the genera *Arctocephalus* and *Callorhinus*. The second group includes species having fur with underfur (fur seals), while those of the first group have no fur.

Of the six contemporary genera, two (*Callorhinus* and *Eumetopias*) inhabit the northern half of the Pacific Ocean, three (*Arctocephalus*, *Otaria*, and *Neophoca*) the Southern hemisphere, mostly the southern parts of all the three oceans including subantarctic waters [*Arctocephalus townsendi* inhabit islands off Mexico in the North Pacific], while the last genus, *Zalophus*, is found in both the Southern and Northern hemispheres.

Two genera are found in the fauna of the USSR: Steller's sea lion, *Eumetopias* Gill, and the northern fur seal, *Callorhinus* Gray. These animals live mainly in the coastal belt of the Far Eastern seas and in the northern part of the Pacific Ocean.

The economic importance of the various genera varies. The genus of northern fur seals (and, to a much lesser extent, the genus of southern fur seals) is of immense economic value for its extremely valuable fur. The rest of the genera of the family are not exploited and have no economic significance. (V.A.)

Key to Species of Eared Seals (Otariidae) [of the USSR]

Identification Based on External Features

- 1 (2). Hand of fore flipper, both on dorsal and ventral surfaces, without hair (totally naked). Narrow tips of lateral (I and V) digits of hind flippers not broader than the three middle ones (II-IV) and slightly shorter. Hair coat on trunk with dense, soft, and silky underfur, better developed in young animals. Length of whiskers in adult males 30-38 cm, in females 20-25 cm.

Body length of adult males from tip of nose to tail end in a straight line (*Lcv*)¹⁰ 135-200 cm, of females 110-150 cm. Color

¹⁰ Not along the dorsal curvature

of adult males dark brown, young males and females silvery-gray, adult females darker with gray streaks.

..... Northern fur seal, *Callorhinus ursinus* (p. 98)

- 2 (1). Hand of fore flippers not entirely naked dorsally, metacarpal region covered with hair. Narrow tips of extreme (I and V) digits of hind flippers slightly longer and broader than the middle ones (II-IV). Hair coat on trunk either lacking underfur or latter scanty.
- 3 (4). Body length of adult males more than 240 cm (up to 340). Head massive, with broad and high snout; forehead of males not steeply raised. Whiskers thick and long (up to 50 cm long and 2 mm in diameter). Color of adult males varies from straw-yellow (in summer) to brown (in winter); females yellowish-brown.
..... Steller's sea lion, *Eumetopias jubatus* (p. 68)
- 4 (3). Body length of adult males less than 240 cm, of adult females less than 185 cm. Head with pointed, longish snout, in males with steeply raised forehead. Whiskers very thin and short. Color of trunk dark, cinnamon-brown to sepia.
..... Californian sea lion, *Zalophus californianus* (p. 92)

Identification Based on Skull Features

- 1 (2). Distance [diastema] between fourth upper premolar and first molar (IV and V) teeth behind canine considerable, approximately twice distance between each adjoining pair of premolars. In males, gap equals 5-8% of condylobasal length of skull. Supraorbital process massive, fairly squarish, its upper outer edge bent slightly accurately outward. Sagittal crest in adults high and long; length of rostral part of skull measured from anterior end of premaxillae to anterior margin of orbit longer than distance from anterior margin of orbit to upper posterior zygomatic process. Condylobasal length of skull in adult males 360-404 mm, in females 290-327 mm.
..... Steller's sea lion, *Eumetopias jubatus* (p. 68)
- 2 (1). Distance between last upper premolar and first molar (IV and V) teeth behind canine not more than between remaining teeth in row, constituting not more than 4% of condylobasal length of skull (males). Supraorbital process triangular with tip turned backward. Arcuate flexure of outer side not seen. Sagittal crest well developed, undeveloped, or extremely small. Length of rostral part of skull same or greater than the distance from anterior margin of orbit to apex of upper posterior zygomatic process. Skull size small.

- 3 (4). Length of rostral part of skull measured from anterior end of premaxillae to anterior margin of orbit more than that from anterior margin of orbit to apex of upper posterior zygomatic process. Nasal processes of premaxillae at level of anterior part of nasals not broadened and gradually taper toward upper end. Sagittal crest in adult males well developed, long and high. Condylbasal length of skull in males up to 330 mm, usually up to 300 mm, in females up to 250 mm. Californian sea lion **Zalophus californianus** (p. 92)
- 56 4 (3). Length of rostral part of skull from anterior end of premaxillae to anterior margin of orbit equal to distance from anterior margin of orbit to apex of upper posterior zygomatic process. Nasal process of premaxillae at level of anterior part of nasals considerably broadened. Sagittal crest absent or very poorly developed. Condylbasal length of skull in males 220-260 mm, in females 180-200 mm. Northern fur seal, **Callorhinus ursinus** (p. 98). (V.H.)

Subfamily of Sea Lions

Subfamily OTARIINAE Böetticher, 1934

Genus of Steller's Sea Lion

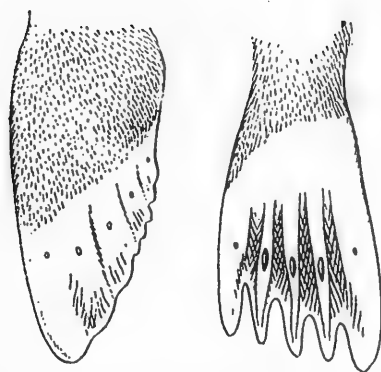
Genus *Eumetopias* Gill, 1866

1866. *Eumetopias*. Gill. Proc. Essex. Inst. 5, p. 7. *Arctocephalus monte-riensis* Gray = *Phoca jubata* Schreber, 1776. (V.H.)

This is the largest member of the family. Males are massive (body length over 3.5 m) and females half as large. The pinnae are small. The fore flippers are covered with fur beyond the metacarpus. The margins of the flippers are represented by a thick, compact coriaceous edge, which is totally bare. All digits of the fore flippers are devoid of claws; the tips of the digits are in the form of round disks (rudiments of claws). On the hind flippers, the two outer digits are without claws (with thickened horny disks); there are three middle digits with well-developed claws (Fig. 33).

The hair coat consists mainly of guard hair; the underfur is either absent or extremely scanty.

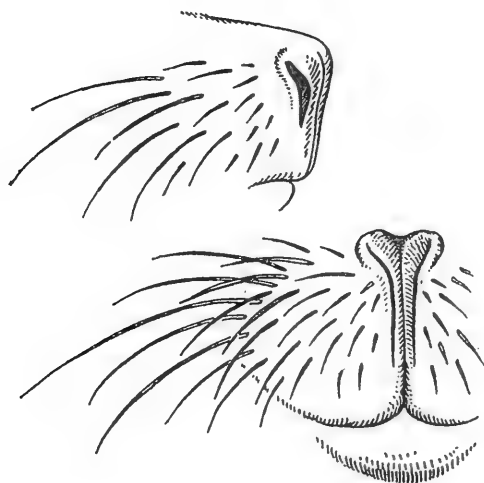
The skull is large, in adult males massive, with large crests; the latter are absent in females. Length of the skull in males exceeds 350 mm, in females up to 300 mm. Anterior portion of the skull at the level of the canines is relatively broad. Suborbital apertures are relatively large. The bony auditory tympana [tympanic bullae] are small and flattened. The



56 Fig. 33. Fore and hind flippers of Steller's sea lion (figure by N.N. Kondakov).

premaxillae gradually narrow toward the apex. The posterior section of the palatines is almost straight or semiarculate. That part of the jaw bearing molars is relatively massive (Figs. 35, 36, 37).

Transverse notches are present on the masticatory surface of the medial upper incisors into which the cusps of the lower incisors fit. The lateral incisors are almost as large as the canines, which are thick and massive. The premolars and molars have simple roots and cusps.

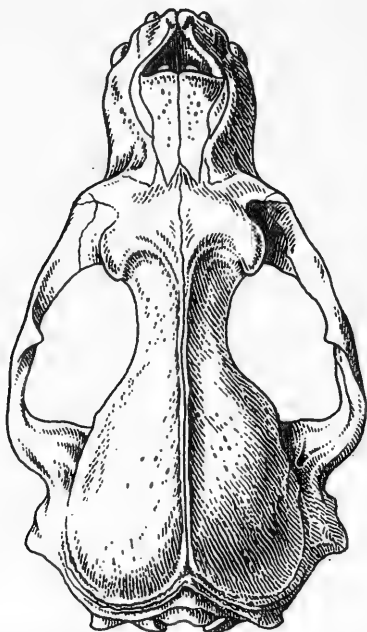


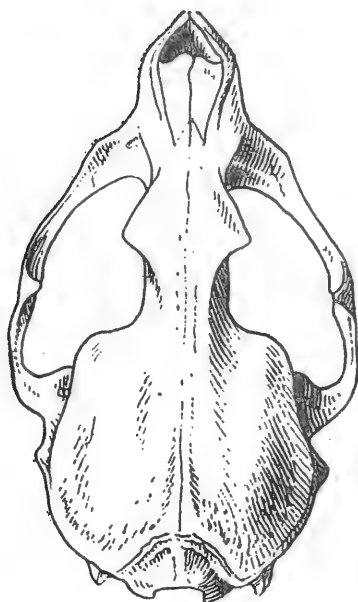
57 Fig. 34. Nostril of Steller's sea lion, *Eumetopias jubatus* (figure by N.N. Kondakov).

The genus *Eumetopias* occupies within the subfamily of sea lions (Otariinae) a position at the commencement of a series of specializations. This is a genus neighboring *Otaria* (southern sea lion), which commences the series of eared seals and thus stands at the base of the series of pinnipeds in general. Being a fully specialized typical form of the order in all respects, this genus of sea lions still bears on its skull the features of land carnivores. This is the most primitive of pinnipeds of the USSR fauna and one of the most primitive in the world fauna.

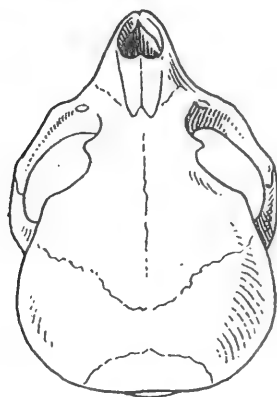
Steller's sea lion is distributed in the warm [cold] and temperate waters of the Northern hemisphere and inhabits the coastal waters of the Pacific Ocean along the Asian and American continents roughly from 33° to 65° N lat. In the west it is found from the coasts of the Korean Peninsula in the south to the northern coasts of the Sea of Okhotsk, 57 eastern coasts of Kamchatka, the Commander Islands, and the Bering Strait. On the eastern coast of the ocean, these sea lions are found from Pribilof Islands, St. Matthew, Nunivak, Aleutian, and other islands in the north to the Californian coasts in the south.

The genus consists of a single species, Steller's sea lion, *Eumetopias jubatus* (Schreber, 1776).





57 Fig. 36. Skull of adult female Steller's sea lion, *Eumetopias jubatus* [dorsal view] (figure by N.N. Kondakov).



57 Fig. 37. Skull of young Steller's sea lion, *Eumetopias jubatus* [dorsal view] (figure by N.N. Kondakov).

58 The economic importance of sea lions is insignificant. In spite of their relative abundance, their hunting is not well organized and only a few are caught in the USSR as well as in other places in the North Pacific Ocean. (V.A.)

STELLER'S SEA LION

Eumetopias jubatus (Schreber, 1776)

1766. *Phoca jubata*. Schreber. Die Sagnetiere, 3, p. 300, Table 83B. Bering Island.
1811. *Phoca leonina*. Pallas. Zoogr. Rosso-Asiat., 1, p. 104. Non Linnaeus, 1758. Japan, Kuril'sk islands, Kamchatka.
1828. *Otaria stelleri*. Lesson. Dict. class. H.N. 13, p. 420. Bering Island. (V.H.)

Diagnosis

Only species of the genus.

Description

The males are large, massive, and heavily built; the females are usually a meter shorter than the males and more slender in appearance. The snout is broad and blunt with a slightly upturned nose. The whiskers are long (up to 30 cm in females, and up to 60 cm in males) and thick (up to 2 mm), on average 69 to 71 [?] cm in length. The neck is long and movable, thick in males, and relatively thin in females. The thick neck of the males is the result of skin folds and long guard hairs on the nape, which perform a protective function during fights with other males.

The hair coat consists mostly of guard hairs. The underfur is sparse, of poor quality, and almost totally absent in old animals.

The color of the hair coat varies depending on the sex and age of the animal and the season. Newborn pups possess a soft pelage. The upper part of the body is dark brown or sandy, gradually turning brown toward the sides; the color is a monochromatic dark chestnut-brown on the belly. There are no color differences between males and females at this stage. The color turns perceptibly lighter after the first molt. Immature juveniles are a light brown. Adult females and males are almost identically colored, the back creamy, the belly dark umber with a creamy tinge, more intense in males. The nape of males is a dark purple but in females creamy. The color of the belly is noticeably darker than that of the back. The winter fur is darker than the summer fur. In winter old males are predominantly chocolate or brown, almost black on the belly. The color gradually becomes lighter in winter; in the summer months (before molt) the upper part of the body is straw-yellow (Nikulín, 1937; A.S. Perlov).

For the skull description, see the description of the genus. The condylobasal length of the skull in males is 367-404 mm (\bar{x} = 389.7), in



Plate I.

Steller's sea lion, *Eumetopias jubatus* Schreber. In the center are an adult male and female. Top—movement of the animals on land and diving into water; bottom—postures of mating and playful behavior, and a group of these animals on a rock in the sea (Kamchatka, Cape Shipunsk, 1973) (figures by V.M. Smirin).

females 308-320 mm ($\bar{x} = 314.7$); zygomatic width in males 211-261 mm ($\bar{x} = 239.8$), in females 176-185 mm ($\bar{x} = 180.9$); maximum width of the skull in males 198-238 mm ($\bar{x} = 223.7$), in females 154-164 mm ($\bar{x} = 160.2$) (Ognev, 1935; Nikulin, 1937; Chapskii, 1963).

The average body length of males is 320-330 cm, of females about 230 cm. Males weigh 700-800 kg (sometimes over 1,000 kg), females up to 320 kg. The average weight of internal organs (for 12 specimens) is: heart 3,233 g, lungs 12,439 g, liver 18,829 g, spleen 526 g, stomach 7,687 g, intestine 21,473 g, kidneys 1,667 g, pancreas 1,420 g, and mesenteries 5,708 g (A.S. Sokolov *et al.*). (V.A.)

59

Taxonomy

See under the characteristics of the genus.

Geographic Distribution

The Steller's sea lion mostly inhabits the coastal belt of the North Pacific Ocean where its distribution is very extensive. The range of the species has undergone no significant change.

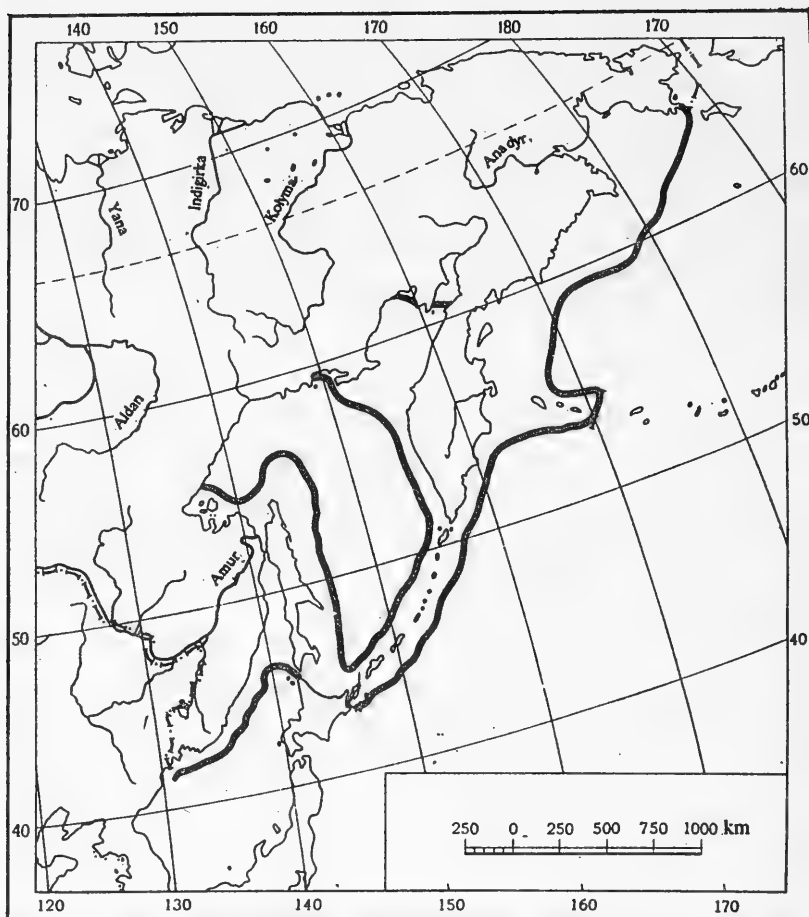
Geographic Range in the USSR

Stray animals and small groups are seen throughout along the coasts of the Sea of Japan, eastern coast of Sakhalin, on Shantar and Kuril islands, northeastern coasts of the Sea of Okhotsk, eastern coast of Kamchatka, and Koryak Land. Rookeries are formed every year on Iony Island in the central part of the Sea of Okhotsk, on Ol'sk and Yamsk islands at the inlet into Shelikhov Gulf, on Kunashir Islands, Iturup, Urup, Simushir, Russhua, Onkotan, Srednev Hills, and Kamennye Lovushki, and on some other islands of the Kuril range; in the Bering Sea at some points on the eastern coast of Kamchatka (on Shipunsk, Kozlov, and Navarin capes), on the Commander, Karaginsk, and Verkhoturov islands. Some rookeries function throughout the year, while some are inhabited only in summer. In the northern part of the Bering Sea animals reach up to the Gulf of Anadyr and the Bering Strait (Fig. 38).

Steller's sea lion has been reported from neither the northwestern part of the Sea of Okhotsk (from Tauisk Bay to Ayan Bay) nor the upper reaches of Shelikhov Gulf.

Geographic Range outside the USSR (Fig. 39)

This species is found on the western as well as eastern coasts of the Pacific Ocean, on the coast of North Korea, and in the Pacific waters of Japan (Hokkaido Island and the northernmost part of Honshu Island).



59 Fig. 38. Range of Steller's sea lion, *Eumetopias jubatus*, in the USSR (V.A. Arsen'ev).

On the Japanese islands, within 35–37° N lat., rookeries of the Steller's sea lion were recorded in the past (Ognev, 1935) but no longer exist today. In the waters of the Korean Peninsula and Japan the Steller's sea lion was observed only in the winter months.

In the eastern part of the Pacific Ocean, Steller's sea lions are distributed from southern California (roughly 33° N lat.) along the entire coasts of the USA and Canada up to the Gulf of Alaska and the Aleutian Islands, and in the eastern part of the Bering Sea from Bristol Bay to the Bering Strait. Permanent rookeries are found on many islands of the Aleutian range (Attu, Kiska, Amchitka, etc.), on the islands of the Gulf of Alaska, on the Pribilof Islands and on nearby Vancouver Island,

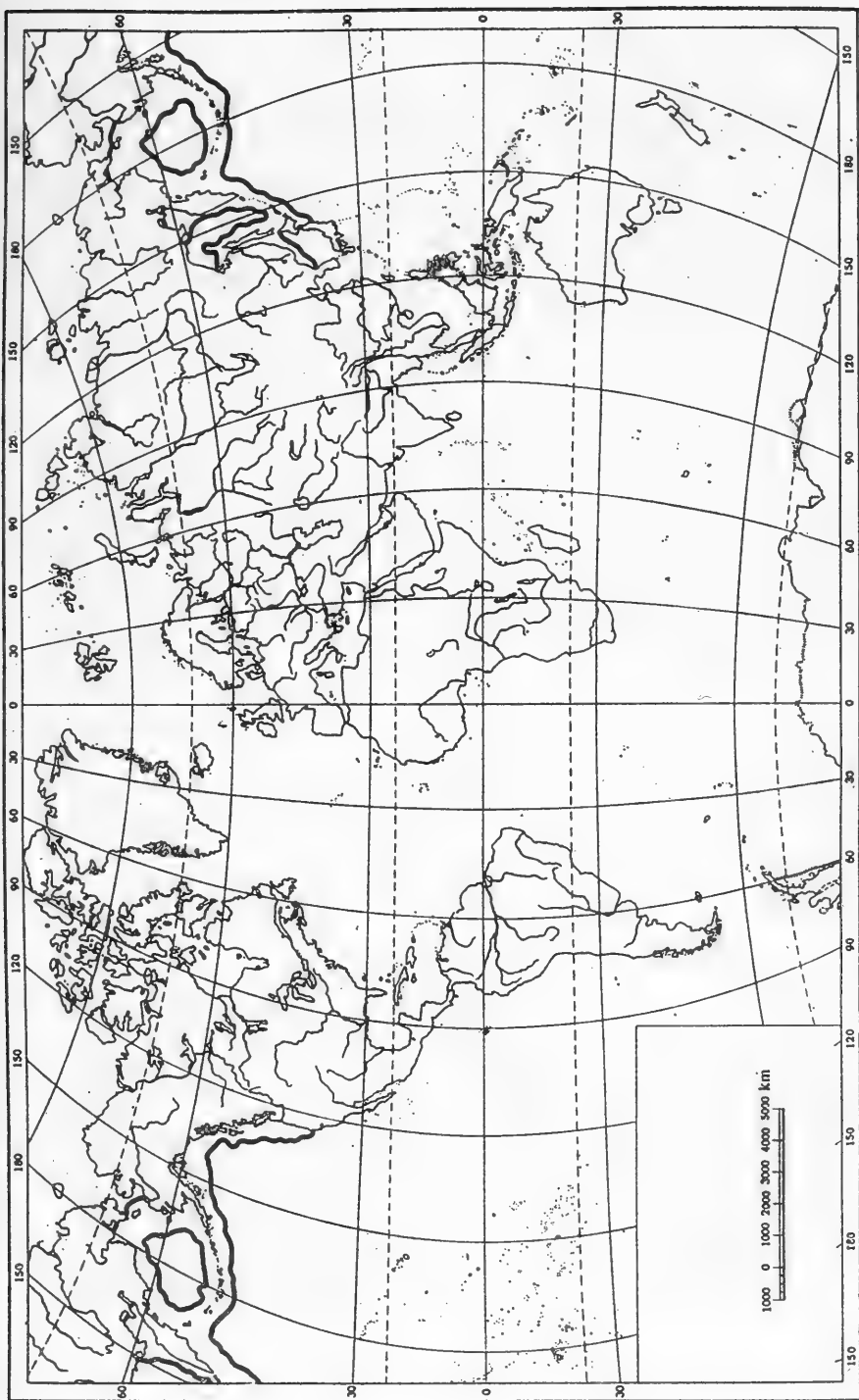


Fig. 39. Species range of Steller's sea lion, *Eumetopias jubatus* (V.A. Arsen'ev).

and also near the coasts of California. Seasonal rookeries are known on the Bering Sea islands (St. Matthew and Nunivak). In many regions the distribution is seasonal (Scheffer, 1958; King, 1964; Nishiwaki, 1966, 1966a).

The ranges of Steller's sea lion and the fur seal lie close by; quite often, these two species form coastal rookeries at one and the same places. The ranges of Steller's sea lion and the walrus almost never overlap. (V.A.)

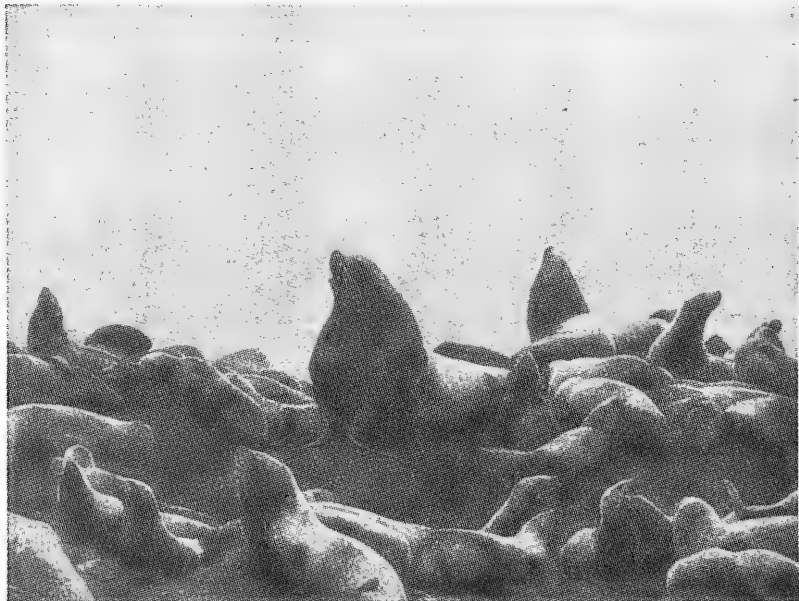
Geographic Variation

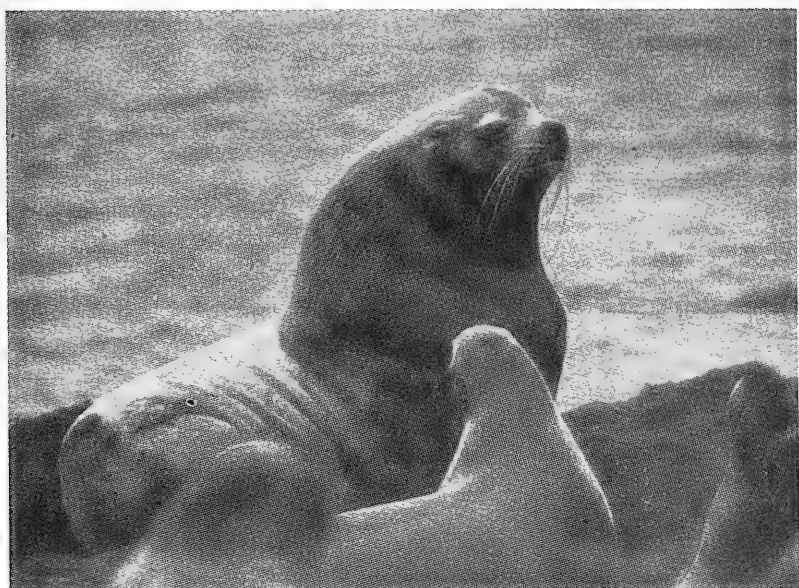
Not established.

Biology

Population. Only a tentative estimate of the total population of Steller's sea lion is possible because the animals present in the coastal rookeries are accounted for but not those swimming in the water. In the northern part of the Pacific Ocean over 160 permanent and temporary rookeries with widely varying populations have been recorded (Fig. 40).

In the USSR waters the maximum number of Steller's sea lions occurs on the Kuril Islands, where 29 permanent and four temporary

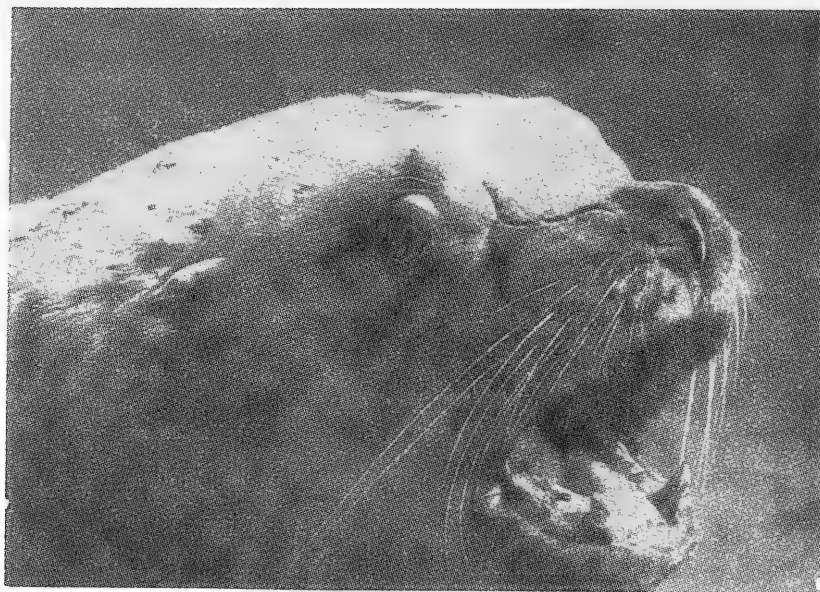




63 Fig. 41. Male and female Steller's sea lion. Mednyi Island, July, 1972 (photograph by S.V. Marakov).

rookeries are known (Urup and Iturup islands, Srednev Hills, etc.) (A.S. Perlov). The total number of Steller's sea lions on the Kuril Islands was determined roughly at 20,000 (Klumov, 1957; Belkin, 1966). On Iony Island in the central part of the Sea of Okhotsk, 3,000-4,000 Steller's sea lions arrive in the summer months. Comparatively large rookeries with a total population of 4,000-5,000 are known in the northeastern part of the Sea of Okhotsk (Yamsk, Ol'sk Islands, etc. at the entrance to Shelikhov Gulf). Small rookeries are known on the coast of northern Sakhalin, but the population of Steller's sea lion there hardly exceeds 1,000. Some ten rookeries of different sizes with a total population of 8,000-10,000 animals are known on the eastern coast of Kamchatka. On the Commander Islands, Steller's sea lion is found quite extensively and its population varies from 4,000-5,000 in summer to 8,000-10,000 in winter (Muzhchinkin, 1964; Nesterov, 1964). Thus the total number of Steller's sea lions in the coastal rookeries of the USSR is 40,000-45,000.

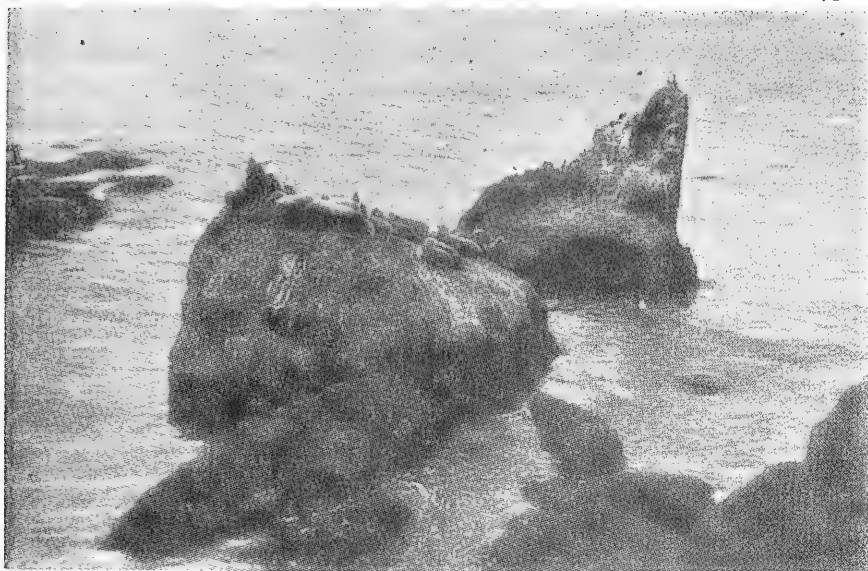
The maximum number of Steller's sea lions inhabit the Aleutian Islands. Here 98 rookeries are known on many islands in different parts of the range, with a total population of 100,000. The population of Steller's sea lion on the Pribilof Islands is around 1,500-1,600. A large rookery



63 Fig. 42. Head of a male Steller's sea lion. Mednyi Island (photograph by F.G. Chelnokov).

on Morzhov Island in Bristol Bay contained 4,000-5,000 animals. The total number of Steller's sea lions on the islands in the Gulf of Alaska is 75,000-76,000, on the coast of British Columbia 11,000-12,000, and on the coasts of Oregon and Washington states 1,000-1,500. Finally, an additional 6,000 live on the coasts of California (Kenyon and Rice, 1961). Thus the population of Steller's sea lion beyond Soviet waters is estimated at 198,000-200,000, with a total of 240,000-250,000.

Habitat. The coastal rookeries of Steller's sea lion are of two types—harems in which reproducing females, males, and pups concentrate, and rookeries of idle animals (bachelors) which do not take part in reproduction. The rookeries are located mostly on almost inaccessible, uninhabited islands or rocky capes. Smooth and level rocky areas are essential for harems and for females to whelp. Large thickets of sea kale and algae grow near most harems. The bachelors' colonies are situated in less convenient sites or along the fringes of harems, most often on rock piles, cliffs, and reefs (Fig. 43). There is no level ground in these rookeries. In many cases, deep waters adjoin these rookeries so that the animals can dive into the sea directly from the cliffs, which are sometimes quite high. The areas of rookeries vary widely, from a few



64 Fig. 43. Habitat of Steller's sea lion. Mednyi Island (photograph by S.V. Marakov).

stray rocks to a large rocky area, depending on the population in the herd, which may range from several tens to thousands.

Food. Fish and cephalopods of no less than 20 species are the two basic food groups of the adult Steller's sea lion. Some geographic variation has been noticed in the food of these animals. In the Californian waters, their stomachs revealed flounder, halibut, and bass; on the Oregon coast (USA): bass, goby, and lumpfish; on the coast of British Columbia: herring, bass, cod, skate, shark, salmon, octopus, squid, bivalves, and once a crab; in the Gulf of Alaska: lamprey, salmon, smelt, sand eel, bass, greenling, goby, shrimp, crab, isopods, squid, and octopus; on the Aleutian islands and in the Bering Sea: pollock, capelin, sand eel, flounder, goby, herring, halibut, greenling, salmon, and mollusks; on the Commander Islands: smooth lumpsucker, cod, greenling, salmon, flounder, and rarely octopus; and on the Kuril Islands: sand eel, greenling, bass, pollock, navaga, goby, flounder, salmon, octopus, squid, and three species of crustaceans (Pike, 1958; Mathisen, Baade and Lopp, 1962; Fiscus and Baines, 1966). Very often stones, sand, gravel, and occasionally algae are found in the stomach of Steller's sea lions.

The commercial species of fish are not usually the mainstay but, with the development of the fishing industry in the Bering Sea, Steller's sea lions have begun to live successfully on human effort. The animals have

developed a conditioned reflex to the working of fishing trawlers. On hearing the noise of a trawl being hauled, the animals in the vicinity quickly gather around the boat, dive into the trawl and feed on the herring. Some animals attempting to get at the fish, damage the net from the outside and spill the catch. The animals have begun to regularly visit the trawlers and sometimes in a single trawl as many as 15 Steller's sea lions have been found (Tikhomirov, 1964).

The feeding grounds of Steller's sea lions are sometimes 50-70 miles (80-112 km) from the coast. In these regions the depth is usually 200 m, but large groups usually feed close to the coasts; only small groups or even stray animals venture far into the open sea. At places of high fish concentrations, the sea lions gather in large herds. Where there are no fish shoals, the sea lions hunt for them alone or in small groups of two to five animals (Fiscus and Baines, 1966).

Steller's sea lions very rarely feed on warm-blooded animals. However, in 1966, close to Yamsk Islands in the Sea of Okhotsk (59° N lat.), the stomach of a large male contained the remains of a young ringed seal weighing 6.8 kg. A Steller's sea lion was caught on an ice floe. In 1959, the stomach of six of the nine sea lions caught contained the remains of seals consumed by them, including adult seals (Tikhomirov, 1959, 1964). It is quite likely that seals are an incidental, rather than a regular food item for the sea lion.

- 65 Steller's sea lion females suckle their pups until they are a year old. It was noticed on the Kuril Islands time and again (more than ten instances) that a female suckled both a newborn and a yearling. The stomach of year-olds often contained milk (up to a liter) though sometimes other foods (beaks of squids and even fish) were found along with milk (Belkin, 1966a). In the Gulf of Alaska, milk was found in the stomach of five-year-olds (of the 17 examined) (Mathisen, Baade, and Lopp, 1962).¹¹

¹¹ A suckling pup held in captivity did not touch food for the first 13 days and had to be force-fed. It later began voluntary feeding. It was given daily 250 to 300 g of rice or beans, 300 to 400 g of meat products, 600 to 900 g of fish, and 30 to 50 g of seal blubber. The food was mixed with boiled water to make up a volume of 5.5 to 7 liters and fed in four or five portions (of 1.5 liters each). The ratio was simplified later. In addition to resting at night, the pup slept in the day after feeding, especially in sunny weather. It soon became quite tame, moved about the camp, entered the tent, and demanded food. It was released in the sea but soon returned voluntarily to the camp. After a month it was brought to Petropavlovsk where it silently accompanied its master through the streets (in spite of the amused crowds and packs of dogs), climbed stairs to a second floor apartment and laid down at the door. A few days later, an unfortunate mishap killed it (Kuleshov, 1950).

Home range. In harems on the beach, a male is surrounded by 5 to 20 females. Each harem has its own distinct area, its size (5 to 20 m² or more) depending on the strength of the harem, total area of the rookery, free zones, animal population, strength and aggressiveness of the male as the head of the harem, and other features. Harems are usually established on comparatively level ground, sometimes even at a height of 10 to 15 m above sea level.

The animals not involved in harem activities stay nearby or on isolated rocks or hill spurs, gathering sometimes at a height of several tens of meters (Fig. 44). From such a height, the huge young males can easily and freely dive headlong into the sea. With the dispersal of the harem, the animals no longer live in age-related groups.

Three types of coastal rookeries have been noticed on the Kuril Islands: harems, herds of maturing young males (bachelors), and juveniles (one- or two-year-olds) (Belkin, 1966).

Daily activity and behavior. On Unimak Island (close to the tip of the Alaskan Peninsula) Steller's sea lions living outside the harems gather early in the morning every day in summer into compact groups of a few hundreds or thousands and set out for the feeding grounds. Here they break into groups of a few tens each and feed throughout the day. Before nightfall they reunite into large groups and return to the rookery (Fiscus and Baines, 1966). The average number of animals seen on the beach in the morning hours (ten observations) was 45 and in the evening (seven observations) 70 (Kenyon and Rice, 1961).

In spring the mature large males (bulls) are the first to appear on the beaches, where they stake out areas for setting up their harems (Fig. 45). Claims lead to severe fights and competition. Next to arrive are the mature females, most of whom are gestating. Harem formation commences, again with fights among rivals. Sometimes after entering the rookery the female undergoes parturition and the mother shields the pup for a few days. Later the females go out to sea for feeding and return to the coast from time to time to suckle the pups. The harem bulls sometimes abandon their harems and go out to sea; their places are immediately taken by other bulls. Whether the bulls that go out to sea return to the harem has not been ascertained. The young of both sexes, not interested in harem activities, make regular visits to the water. The harem bulls keep the harmless bulls and young males at bay by chal-
 66 lenging them at the first sign of encroachment (Fig. 46). By June end the harem bulls become more tolerant and pay no attention to other bulls in the first half of July, when the harem has disbanded.

In the rookery, the animals are restless and groan incessantly; their groaning can be heard for miles. The adult male groan is a deep-drawn



66 Fig. 44. Steller's sea lion, *Eumetopias jubatus* on a cliff (photograph by S.V. Marakov).

bass, somewhat like the distant siren of a ship, while that of a female is shrill and penetrating, somewhat like the mooing of a cow. The pup's yell is quite shrill and booming, like the bleat of a sheep (Nikulin, 1937). In the rookeries (mainly bachelor zones) traffic from the coast to the sea and back is quite regular. This movement intensifies correlated with the disbanding of the harems. In stormy weather bulls outside the harems prefer to be at sea, while those on the beach try to gather on cliffs far away from water; in a prolonged storm, having spent a few hours on the beach, they, too, take to the sea but remain close to the coast.

Sometimes, Steller's sea lions are noticed on ice floes where they remain quite at peace. Animals swimming in the sea are mostly engaged in seeking food.

Seasonal migrations and transgressions. Steller's sea lions obviously do not undertake distant migrations, as they are relatively well-settled



67

Fig. 45. Large male Steller's sea lion (photograph by S.V. Marakov).

animals. In many regions their coastal rookeries function throughout the year (South Kuril, Commander, and Aleutian islands); however, the animal population in these rookeries fluctuates seasonally.

Nevertheless, seasonal rookeries are established in the northern parts of the range in summer, but are wholly abandoned in winter. In the Sea of Okhotsk (Iony and Yamsk islands) seasonal rookeries are occupied by animals of various ages and sex groups, harems are formed, and pups born. On the Bering Sea islands (Nunivak, St. Lawrence, and St. Matthew) bachelors form exclusive rookeries; no females have ever been sighted in them. In these cases the Steller's sea lions perform regular seasonal migrations, evidently for relatively short durations, although their wintering sites have not been confirmed. The main reason the animals abandon these islands is the appearance of dense floating ice floes.

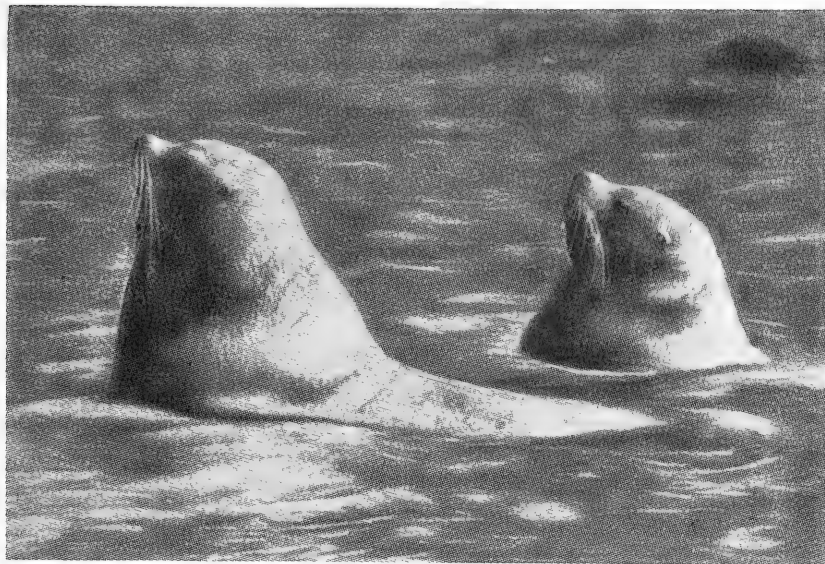


68 Fig. 46. Rookery of bachelor Steller's sea lion, *Eumetopias jubatus*; at the center is a bull northern fur seal, *Callorhinus ursinus*. Mednyi Island, June, 1969 (photograph by S.V. Marakov).

On the Commander Islands the sea lion population in winter is considerably higher than in summer. Here mainly young males are seen
 67 although sometimes groups resembling harems occur but without fights among males as in harems. In 1966-1967, a gradual increase in the population of males and adult females was recorded on the Commander Islands, while in 1968, the gradual appearance of adults in the rookeries on Mednyi Island was recorded. The formation of genuine harems has not yet been recorded but observations over decades have confirmed a few cases of newborn pups. Evidently the change in population of sea lions on the Commander Islands is associated with their migration from the rookeries on the eastern coast of Kamchatka (Chugunkov, 1968; G.F. Chelnokov).

Thus, though Steller's sea lions do not undertake regular seasonal migrations, there are regular local wanderings around all the rookeries.

Only a few relatively long transgressions of this sea lion are known. From time to time, stray animals appear in the northern part of the Bering Strait on the Diomide Islands (approximately 66° N lat.). The



68 Fig. 47. Steller's sea lions in water. Mednyi Island (photograph by F.G. Chelnokov).

reported case of a sea lion on Herschell Island in the Chukchi Sea (69° N lat.) has not been properly verified (Kenyon and Rice, 1961).

Reproduction. Females begin to arrive at the rookeries from May end to early June, roughly two to three weeks after the males have arrived. Sometimes, immediately upon arrival, or after a few days, the females undergo parturition, each giving birth to a single pup. After a few days the female is mated by a bull. In between birth and mating the bull does not permit the female to leave his harem and only after fertilization does she begin going out to sea, returning periodically to suckle her pup.

The arrival of females at the rookery is not simultaneous and hence the periods of birth and mating are somewhat protracted: roughly from the end of May to early June to the end of June. On Chernabur Island in the Gulf of Alaska, the first births were recorded on May 24 and the last on June 27 (Mathisen, Baade, and Lopp, 1959*). Since mating occurs a few days after parturition, gestation obviously extends for about a year and parturition is perhaps an annual affair. In spite of the harems being disposed extremely far away from each other along the latitude and longitude, the periods of reproduction at various places are quite close. Whelping on the Kamchatka coast occurs in June (Sleptsov, 1950), over much of June on the Kuril Islands (Belkin, 1966), from May 23 through June 27 on the Aleutian Islands and in the Gulf of Alaska (Scheffer, 1945;

- 69 Mathisen, 1959), and from May end through June end on the coast of British Columbia (Pike and Maxwell, 1958).

Growth, development, and molt. In Steller's sea lion the period of latent development of embryos extends 2.5-3 months and fetal growth takes place for 9-10 months. Before birth the embryos grow very large. A female 246 cm in length contained an embryo 94 cm long weighing 12 kg on May 14; an embryo 105 cm long weighing 15 kg was found on May 19 in a female 234 cm in length; another female, 230 cm in length, contained an embryo 100 cm long weighing 16 kg on June 2 (Sleptsov, 1950).

The length of newborns at 100-120 cm is roughly half the body length of the mother and they weigh 17-20 kg. For the first few hours the pup is altogether helpless but soon begins to move independently all over the rookery. In the first 7-10 days these movements are highly restricted but 25-30 days after birth (Fig. 50) pups move about freely in water and, by early August, easily cross the channels between cliffs (Belkin, 1966).

Pups grow very fast and size differences between the sexes are discernible almost from birth. On the eastern coast of Kamchatka, on June 4 and 6, measurements of 73 pups 10-15 days old were taken. Males varied in length from 104-121 cm and females 101-116 cm. A male 107 cm long weighed 24.8 kg, while a female 104 cm long weighed 27.6 kg [sic] (Sleptsov, 1950). On Iony Island, on July 23-25, 1933, the body length of 1-1.5-month-old males varied from 125-138 cm and their weight from 27-44 kg; the corresponding values for females were 112-132 cm and 24-36 kg (Nikulin, 1937). The subsequent growth of pups was not studied.

The average length of yearlings from Alaska was 175 cm (Mathisen, 1959) and their further growth is given in Tables 4 and 5.

These sea lions cease to grow perhaps at the age of 15-20 years. Of the seven sexually mature males caught on Iony Island, the smallest was 228 cm long and the largest 353 cm, while the corresponding values for adult females were 170 and 263 cm. A male 345 cm long weighed 768 kg and a female 263 cm long weighed 208 kg (Nikulin, 1937).

- The earlier established period of the onset of maturity for females of the Sea of Okhotsk at two to three years (Nikulin, 1937; Sleptsov, 1950) is rather doubtful. The youngest reproducing female (on Chernabur Island), with a length of 245 cm, was nine years old; the 265 cm long oldest female 70 was 22 years of age. The youngest mating male was five years old and the oldest (320 cm) was 19 years old (Mathisen *et al.*, 1959*). The life span of the Steller's sea lion has not been established.

69 **Table 4. Change in body length (cm) with age in male Steller's sea lions on Vancouver Island (Fiscus, 1961)**

Age	No. of animals studied	Average length	Age	No. of animals studied	Average length
1 year	1	178	11 years	3	295
2 years	—	—	12 years	4	299
3 years	2	208	13 years	—	—
4 years	—	—	14 years	—	—
5 years	1	272	15 years	2	317
7 years	1	262	16 years	2	325
8 years	2	310	17 years	—	—
9 years	4	288	18 years	—	—
10 years	3	301	19 years	1	317

70 **Table 5. Change in body length (cm) with age in female Steller's sea lions in British Columbia (Spalding, 1964)**

Age	No. of animals studied	Average length	Range of length
Newborn	9	100	90-105
3 months	5	120	110-130
9 months	1	160	
1 year	23	164	130-202
2 years	3	180	163-189
3 years	3	207	190-221
4 years	5	213	198-233
5 years	5	223	196-244
6 years	6	227	220-232
7 years	7	230	210-242
8 years	5	235	228-245
9 years	7	232	206-254
10 years	7	235	221-246
11 years	8	232	216-254
12 years	6	240	226-254
13 years	7	230	216-244
14 years	5	236	204-249
15 years	6	244	234-253
16 years	6	243	236-246
17 years	2	243	236-249
18 years	4	239	218-257
19 years	3	248	245-251
20 years	1	239	
20+ years	4	241	218-254

The newborns are covered with dark brown soft hair. After molting of the juvenile hair, the fur becomes somewhat lighter; however, the light brown color persists in the juveniles. Adults sport a rust-colored coat while the very old animals have straw-yellow fur.

Periods of annual molt have not been established but are believed to extend from August through November (Nikulin, 1937).

Enemies, diseases, parasites, mortality, and competitors. At sea, killer whales are the main enemies of sea lions, mostly attacking the young. Some rookeries are threatened by the brown bear, which is dangerous only for the young. Diseases and natural mortality have not been studied. Many pups perish during storms, when waves lash the beach and carry away the newborns incapable of swimming. During fights among harem bulls the tiny pups get crushed and die.

The ecto- and endoparasites of the sea lion are diverse. Two species of mites have been found in the nasopharynx: *Orthohalarachne attenuata* Newell, 1947 and *Orthohalarachne fluctus* Newell. Lice, *Proechinophthirus fluctus* (Ferris) and *Antarctophthirus microchir* (Trouessart and Newman), parasitize the skin.

Of the 13 species of helminths found in the Steller's sea lion, two were cestodes, seven nematodes, and four acanthocephalans. Trematodes were not detected. The cestodes, *Anophryocephalus ochotensis* Delamure and Krotov (known only in Steller's sea lion) and *Diplogonoporus fasciatus* (Krabbe), parasitize the intestine. The nematodes, *Anisakis tridentata* Kreiss (not known in other pinnipeds but found in many species of whales) and *Anisakis similis* (Baird), localize in the stomach. The stomach and small intestine of this sea lion are parasitized by *Contracaecum osculatum osculatum* (Rudolphi) (known from many other species of pinnipeds in the Northern and Southern hemispheres). *Terranova decipiens* (Krabbe) is widely prevalent in pinnipeds and whales. *Parafilaroides nanus* Dougherty and Herman and *Parafilaroides proficus* Dougherty and Herman, parasitizing the lungs, are found only in this sea lion. *Uncinaria lucasi* Stiles has been found in the intestines of an underyearling.

Among the acanthocephalans, *Bolbosoma bobrovi* Krotov and Delamure parasitizes the small intestine of the sea lion and the Kuril fur seal. *Corynosoma villosum* van Cleave (widely distributed in marine and
71 land mammals), *Corynosoma strumosum* (Rudolphi), and *Corynosoma ventronudum* A. Skrjabin have been found in the intestines of the sea lion.

The mite *Orthohalarachne diminuata* Newell was detected in the trachea and bronchi of the Steller's sea lion (Ass, 1934; Margolis, 1954; Delyamure, 1955; A. Skrjabin, 1948).



71 Fig. 48. Young Steller's sea lion with a fur seal. Mednyi Island (photograph by S.V. Marakov).

Sea lions compete with fur seals, which are ecologically proximate to them during residence in the coastal rookeries (Fig. 48). Otherwise, these two species are quite isolated from each other. In the coastal rookeries, fur seals and sea lions compete in territorial fights for harems. These are most distinctly seen in the small rookeries of the Kuril Islands, where harems of sea lions and fur seals are formed at the same sites. Competition is seen less elsewhere. The breeding period of the sea lion commences somewhat earlier than that of the fur seal. When the harem periods of the two species coincide, the sea lions (being larger and more powerful) drive away the fur seals from the adjoining rookeries and prevent the formation or spread of fur seal herds. However, the harem period of sea lions is relatively short and their harems begin to disband usually by the end of June. At this time, the pups of the sea lions begin moving freely in water, some adults move to other sites, and the number of Steller's sea lions in the rookeries considerably declines. Among the fur seals, however, harem activity is at its zenith by this time and they are no longer threatened by the sea lions as in the second half of June. Thus they are able to freely enlarge their harems and supplement the number of fur seals taking part in reproduction. The

sea lions entering the rookeries of the fur seals unceremoniously disturb their harem regime with utter contempt for the aggressive fur seal bulls. However, the sea lions themselves do not exhibit much aggression and simply suppress the fur seals by their mere physical bulk (Belkin, 1966a).

73 A few thousand Steller's sea lions, with young ones predominant among them, inhabit the Commander Islands in summer. However, some old males and adult females are also found there. Sometimes even small harems are formed. In winter and spring the sea lions occupy fur seal rookeries but have almost completely vacated them by the time the fur seals are in heat. The two species coexist quite peacefully on the Commander Islands, with no aggressive competition (Fig. 49). On the Pribilof Islands (Alaska), compared with the millions of seals, the sea lion population is so small that the former completely dominate them and thus the latter exert no influence whatsoever on life in fur seal rookeries.

Such then are the historic relations between the two species of eared seals in the areas of their cohabitation. They coexist relatively well during



the most important period of their annual life cycle, i.e., in the period of reproduction.

Steller's sea lions and fur seals share many items of food, but their competition in this field is not at all clear (see under "Enemies, Diseases, Parasites, Mortality, and Competitors" in the section "Fur Seals").

Population dynamics. In some parts of the range, significant changes in Steller's sea lion populations have been noticed in recent decades, essentially as a result of human intervention. Mention should be made first of one of the largest rookeries on Iony Island in the Sea of Okhotsk, rookeries on Yamsk Islands (northeastern part of the Sea of Okhotsk at the entrance to Shelikhov Gulf), and some on the eastern coast of Kamchatka. At the same time, on the Kuril Islands where sea lions are not hunted, there has been a steady increase in the number of rookeries and population of animals in them. Over the rest of the extensive range, population fluctuations, mainly due to natural factors, are insignificant.

At present, it is the complex of natural factors that exclusively affects the population of sea lions in our [Northern] hemisphere and they are practically unaffected by human intervention (there is almost no hunting of sea lions).

Field characteristics. Steller's sea lion, one of the largest members of the order Pinnipedia, is larger than other species of the family of eared seals. Its canines are comparatively massive and of the same size in the upper and lower jaws; there are no tusks as in walruses. The pinnae are small but distinct (Fig. 50).

In the period of residence on the beaches, when the natural color of
74 the dry animals can be seen, adults are of different shades of rust; by the end of summer, the hair coat on the neck, shoulders, and back becomes straw-yellow, on the flanks light rust, and on the belly rusty. Females are somewhat darker than males. The bulls groan in a deep bass, reminiscent of a ship's siren, while the groan of adult females and young ones sounds like the mooing of cows, and the voice of an underyearling like the bleat of a sheep. The noise in the rookery can be heard miles away.

Sea lions mainly rest on individual rocks and cliffs (excluding harems), gathering quite often along cliff projections at a great height. The animals dive easily into water from precipitous coasts, from heights of 10 m or more (Fig. 51).

Economic Importance

There has been no state hunting for Steller's sea lion for over 20 years. Local hunters use only some rookeries accessible to them and so some



72 Fig. 50. Steller's sea lion pup. Kuril Islands, July, 1962 (photograph by G.M. Kosygin).

herds have not been exploited at all. In view of this, the economic importance of Steller's sea lion is negligible.

This sea lion is hunted by different methods, including the use of rifles. Butchering a large sea lion shot among huge boulders is a difficult task, requiring many hours of hard work.

The raw material obtained from Steller's sea lion, like that from other marine animals, can be used quite completely. The skin of the sea lion serves as a good raw material for making leather goods. Local hunters greatly value articles made from the skin of the sea lion. The meat of a young sea lion has an excellent flavor while the meat of other age groups is satisfactory as food for fur-bearing animals. Locals use it as food for their sledge dogs. The oil melted from the blubber is useful in tanneries and a few other industries. The endocrine glands serve as excellent raw material for making hormonal endocrinal preparations, and vitamin A is produced from the liver fat.

Steller's sea lions are few in number and their reproduction tempo is slow; hence the utilization of their stocks should be planned rationally. The formation of compact coastal rookeries facilitates rational exploitation of the sea lion, primarily by separating the animals into age and sex groups. The young males (bachelors) which are in excess for a polygamous mode of life, should be the main target followed, perhaps, by some adult males. (V.A.)



73 Fig. 51. Steller's sea lion diving from a cliff. Mednyi Island (photograph by F.G. Chelnokov).

Genus of Northern [or California] Sea Lions¹²

Genus *Zalophus* Gill, 1866

1866. *Zalophus*. Gill. Proc. Essex. Inst., Salem, Communications, 5, p. 6.
Otaria gilliespii MacBain = *Otaria californiana* Lesson.

The body size is moderate, smaller than Steller's sea lion (*Eumetopias*) but larger than the fur seal (*Callorhinus*).

The hind flippers are shorter than the fore flippers, their length less than a quarter of the body length; the outer digits (I and V) on the hind flippers are somewhat longer and broader than the middle ones (II-IV).

75 The upper surface of the hand is naked only terminally; the basal half of

¹² In view of the unusual presence of these sea lions among the Soviet fauna (see below), a brief description of the genus as well as the species is given, which suffices for identification. The morphology is mainly taken from V.B. Scheffer (1958), M. Nishiwaki and F. Nagasaki (1960), K.K. Chapskii (1963), J. King (1964), etc. (V.H.)

it is covered with hairs. The undersurface of the hand is wholly naked. Dense silky underfur is either altogether absent or very sparse. The color is dark, monochromatic.

The skull is relatively narrow and elongated. Its rostral part, measured from the anterior end of the premaxillae to the anterior margin of the orbits, is more than the distance from the anterior margin of the orbits to the upper posterior process of the zygomatic bone. The profile of the nostrils resembles a hollow inclined line (not forming a sharp projection). The supraorbital processes are triangular with a pointed apex turned backward. The nasal processes of the premaxillae are not enlarged in the region of contact with the anterior parts of the nasal bones, and narrow uniformly toward the upper end. The sagittal crest in males is very high and long, commencing in the interorbital region.

The dental formula is:

$$I \frac{3}{2}, C \frac{1}{1}, P \frac{4}{4}, M \frac{2-1}{1} = 36-34.$$

The wide gap [diastema] between the last upper premolar and the first molar (teeth IV and V behind the canine) is lacking, the distance between them being the same as between the premolars, which is not more than 4% of the condylobasal length of the skull (males). The lateral incisors are massive, tusklike, and the crowns of the cheek teeth are conical with undeveloped or faint lateral cusps. The first true upper molar (M') has one root.

These sea lions represent a form which is relatively close to Steller's sea lion (*Eumetopias*). Further relations bring it close to the Australian sea lion (*Neophoca*) and the southern sea lion (*Otaria*). They are usually grouped together in the subfamily Otariinae, rather than in the group of fur seals comprising southern (*Arctocephalus*) and northern (*Callorhinus*) fur seals forming the subfamily Arctocephalinae. Thus this sea lion has very little in common with our fur seal.

The California sea lion genus is ancient; its phyletic links can be traced in the Miocene.

Its range extends into the North Pacific Ocean between the equator and 49° N lat., with three isolated populations (Fig. 52): 1) along the American coast (California to British Columbia); 2) the Galapagos Islands; and 3) the Sea of Japan and the Pacific coast of the Japanese islands.

The genus consists of only one species, the California sea lion, *Zalophus californianus* Lesson, 1828.

This species appears (appeared ?) incidentally in the USSR waters in the southern part of the Far East. (V.H.)

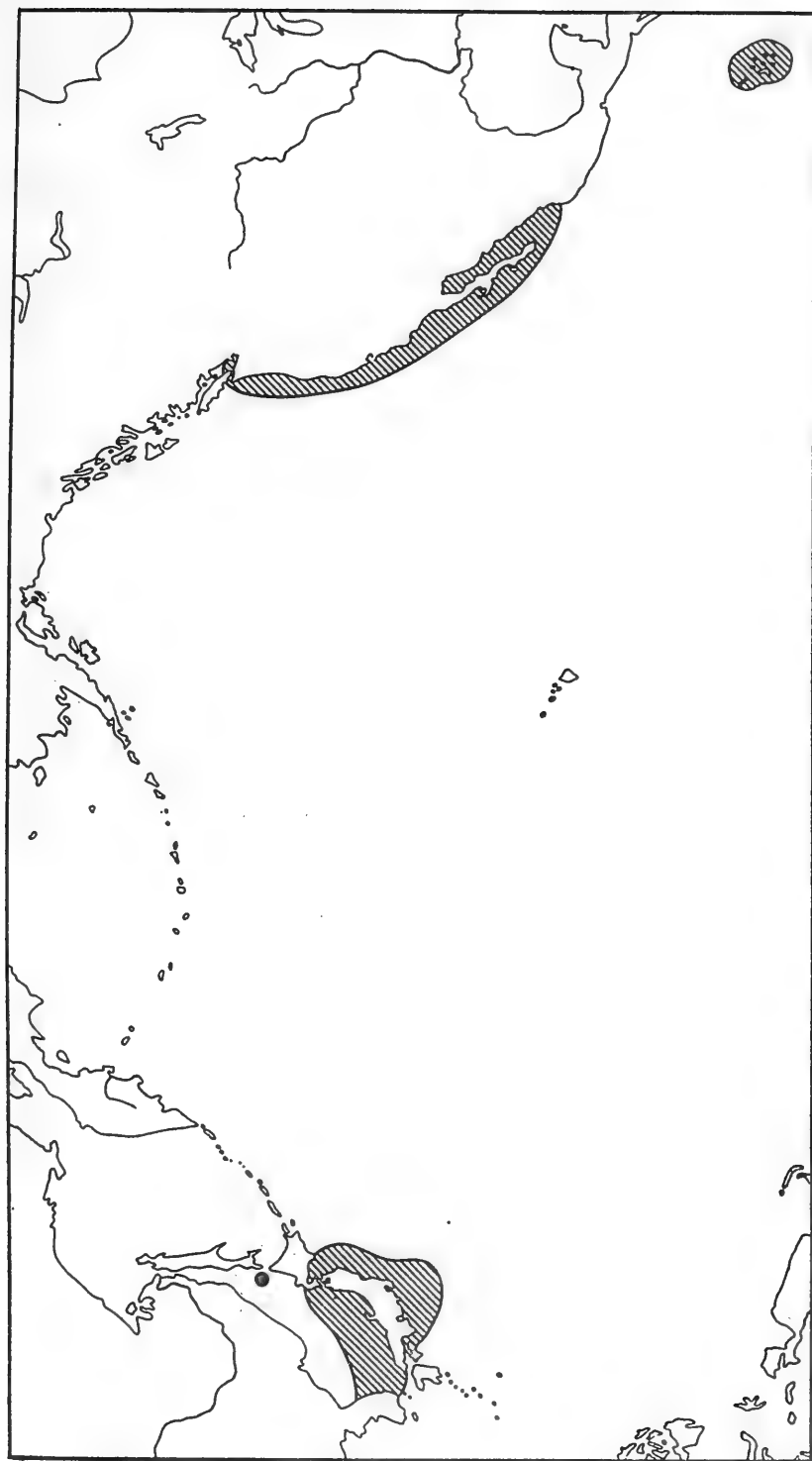


Fig. 52. Range of the California sea lion *Zalophus* and the Californian species of sea lion, *Z. californianus*. Dot at the southwestern tip of Sakhalin indicates the find at Moneron (V.G. Heptner).

CALIFORNIA SEA LION

Zalophus californianus (Lesson, 1828)

1828. *Otaria californiana*. Lesson. Diction. class. Hist. Nat., 13, p. 420. California.
1858. *Otaria gilliespii*. MacBain. Proc. Edinb. R. Phys. Soc., 1, p. 422. California.
1866. *Otaria japonica*. Peters. Monatsschr. K. Preuss. Akad. Wiss., Berlin, p. 669. Sea of Japan. (V.H.)

77

Diagnosis

Monotypical species of the genus.

Description

This sea lion differs from fur seals and especially from Steller's sea lion in its lighter and more slender general build; thin, elongated, and flexible body; and very long and movable neck. The anterior part of its body is not as massive as in the other aforementioned species. The head of the males has a sharp snout and a sharply raised forehead, as a result of the development of the sagittal crest (Fig. 53). Females have a gentler upper line of profile, and the head, on the whole, appears slender and elongated. The whiskers on the upper lip are long and directed downward.

The appearance of the female has much in common with the female fur seal but apart from some large overall dimensions, differs in the shortened and more hairy hind flippers, and elongated head with a broader snout.

- 78 The color of the California sea lion is very dark, varying from dark brown of different shades to sepia. An animal with wet fur appears almost black. With age, the head becomes somewhat lighter in color.

The skull (see characteristics of the genus) is elongated, with a long rostrum, elongated nasals, and relatively close-set zygomatic arches (Fig. 54). The interorbital constriction is elongated; the cranium is relatively small and slightly bulged.

The body length of adult males (in a straight line from tip of nose to end of tail, *Lcv*) is 215-230 cm, of females 160-185 cm; weight of males 230-315 kg, of females up to 100 kg. The condylobasal length of the skull of adult males measures up to 330 mm, of females up to 251 mm. (V.H.)

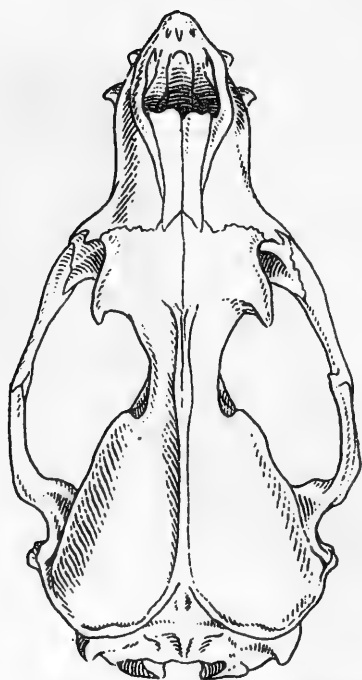


77 Fig. 53. California sea lion, *Zalophus californianus* (figure by N.N. Kondakov, after the American form of the species).

Geographic Distribution and Geographic Variation

The distribution of the California sea lion (see under characteristics of the genus) is considerable because its range is divided into three sections located far from each other. This is one of the rarest cases of an interrupted range of species among mammals. While the distance between the west American (Californian) and Galapagos ranges is about 2,000 km, that between the Californian and Japanese ranges is separated by the whole of the Pacific Ocean (along 40° N lat.), i.e., about 8,000 km. Nevertheless, the species identity of the three populations is indubitable.

The following populations are regarded as special subspecies: 1) *Z. c. californianus* (Lesson, 1828)—Pacific coast of North America from the southern tip of the Californian Peninsula (Las Tres Marias Island, about 21°30' N lat.) to the southern part of British Columbia at 49° N lat.

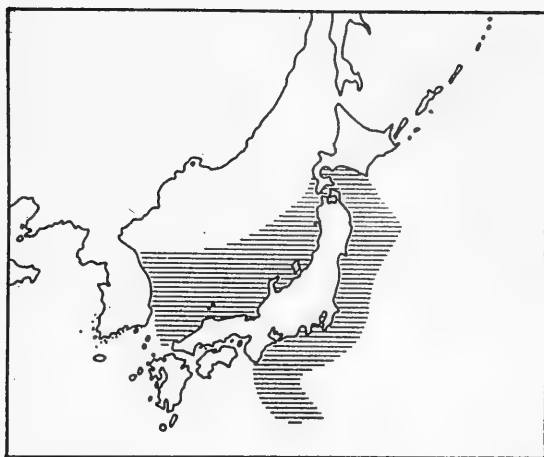


77 Fig. 54. Skull of the California sea lion, *Zalophus californianus* (figure by N.N. Kondakov).

(reconstructed range); 2) *Z. c. wolfebaeckii* (Sivertsen, 1953)—Galapagos Islands; and 3) *Z. c. japonicus* (Peters, 1866).

The Japanese sea lion is distributed on the eastern coasts of the middle part of the Korean Peninsula, on the western coasts of Honshu Island, along its eastern coasts, on the southern coasts of Hokkaido, and in Sangar Strait (Fig. 55). The range further includes the entire southern part of the Sea of Japan and that part of the Pacific Ocean adjoining Honshu, usually not more than a few kilometers from the coast (Nishiwaki and Nagasaki, 1960). Apparently the range was more extensive in the past.

The California sea lion is usually not included in our fauna (Smirnov, 1908; Ognev, 1935; Bobrinskii, Kuznetsov, and Kuzyakin, 1965); however, there is one reference to its possible appearance in our waters (Chapkskii, 1963). Reports of its presence in our waters should be considered reliable. The reference is not to permanent presence or regular sightings, but to irregular transgression of individuals. Such is the reference (Kuroda, 1938, under the name *Eumetopias gillespii*, cited from Ellerman and Morrison-Scott, 1966*) to the sighting of this species on



78 Fig. 55. Range of the Japanese sea lion, *Zalophus californianus japonicus* (from Nishiwaki and Nagasaki, 1960).

the Kuril Islands. One sea lion was killed at the end of March or early April, 1949, on the rocks in the eastern extremity of the small Moneron Island in the Sea of Japan, slightly west of the southwestern extremity of Sakhalin, by the keeper of the lighthouse, D. Barabash. The animal was alone. Its skin, very badly damaged, was examined in July of that year by the zoologists of Sakhalin Institute, Academy of Sciences, USSR, A.I. Gizenko and V.G. Voronov, who immediately recognized it as that of a sea lion. "The general color of the skin is brown, slightly cinnamonic, and a dark band 3-5 cm wide runs from the tip of the nose to the sin-
 79 ciput [forehead]. The orbital apertures in the skin are surrounded by pale bands 3-4 cm wide; there is a flesh-colored spot 3-4 cm in diameter below each of these apertures with a slight singeing. Long hairs, characteristic of Steller's sea lion, are lacking on the nape" (from the diary of A.I. Gizenko, entry of July 10, 1949; letter dated June 9, 1973; V.G. Voronov). One live animal, possibly of this species, was sighted in the northern part of Shiashkotan Island (northern Kurils) in November, 1970, and in 1967, a carcass torn by wolves was found on the shoals in the northern part of Kambal'ny Bay, west of the southern tip of Kamchatka (V.G. Voronov). The last instances pertain to the far northern latitudes and are highly dubious but the appearance of the Californian sea lion on Moneron is quite possible. As far as we are aware, there is no museum material confirming the presence of the Californian sea lion in our waters.

There is good justification to assume the presence of this species in our waters, as the northern boundary of the zone of its permanent habitation or appearance falls on the latitude of Vladivostok and conditions, at times, facilitate its northward penetration. Such conditions can arise during intense warm currents, with which this species is evidently associated in the Sea of Japan. Thus instances are known in Vladivostok of the appearance of sea snakes (*Pelamys platurus*) and turtles (*Dermochelys coriacea* and *Caretta caretta*), which normally inhabit far more southern horizons than sea lions and fish. Drifting carcasses have also been seen. (V.H.)

Biology

The population of the Japanese sea lion has evidently always been low but has declined sharply in this century. In the early 1950s, its population was estimated to be 200-500 and, in 1958, roughly 200 (Scheffer, 1958). According to some recent information (Nishiwaki, 1972*), they had possibly vanished altogether by the early 1970s. In any case, "the absence of sightings. . . in the last 30 years suggests the disappearance of this species, though it is possible that some individuals may have survived on the eastern coast of the Korean Peninsula" (Nishiwaki, 1974).

Data are not available on the biology of the Japanese form. In the breeding period the animals are confined to the rocky coasts, mainly of islands, and form harems. The rest of the time is spent mostly at sea. They feed on fish and cephalopods. (V.H.)

Subfamily of Fur Seals

Subfamily ARCTOCEPHALINAE Böetticher, 1934

Genus of Northern Fur Seals

Genus *Callorhinus* Gray, 1859

- 1859. *Callorhinus*. Gray. Proc. Zool. Soc. London, p. 359. *Phoca ursina* Linnaeus.
- 1866. *Arctocephalus*. Gill. Proc. Essex. Inst. 5, p. 11, Nec Geoffroy Saint-Hilaire et Cuvier, 1826 (*A. pusilus* Schreber, 1776).
- 80 1892. *Callotaria*. Palmer. Proc. Biol. Soc. Washington, 7, p. 126. Substitute for *Callorhinus* Gray. (V.H.)

The males are large and heavily built, while the females are much smaller and more elegant. The pinnae are small but longer than in the much larger Steller's sea lion, narrow, and somewhat pointed.

Claws are absent on all five digits of the fore flippers and replaced by small horny disks. The outer digits of the hind flippers on which likewise no claws are present, are only slightly shorter than the inner ones with well-developed long sharp claws.

The hair coat consists of guard hair and dense soft underfur, better developed in the young. The color of the hair coat depends on the age and sex (see below under "Description").

The skull is moderate in size, its length in adult males being less than 300 mm (equal to that of the female Steller's sea lion). Crests are not prominent. The anterior part of the skull is of moderate width. The cranial capsule is spacious and relatively high. The bony auditory tympana [tympanic bullae] are very small and flattened.

The lateral incisors on the upper jaw are slightly longer than the medial ones. The canines are relatively large and sharp, and the sizes of the upper and lower ones are almost identical; the upper canines do not grow into tusks. The molars and premolars have conical crowns and simple single roots. The skull of the male is larger, more massive, and with more prominent crests than that of the female.

These polygamous animals gather in large, dense coastal rookeries in summer. They undertake seasonal migrations.

The genus *Callorhinus* is one of the highly specialized genera of the family and is usually regarded (Scheffer, 1958) as the culminating link in the chain of genera of eared seals.

These are inhabitants of temperate and cold waters of the North Pacific Ocean where they are encountered on the western and eastern coasts. In the western part, they are seen from the Sea of Japan (up to 36-37° N lat.) and the coastal belt on the eastern coast of Japan (36-38° N lat.) to the central part of the western coast of the Bering Sea (Olyutorsk Bay, 60° N lat.), inhabiting the waters of the Sea of Japan, the southeastern coast of Sakhalin, the Kuril Islands, near the eastern coast of Kamchatka, and the Commander Islands. In the eastern part, they are seen from the coasts of California (33-35° N lat.), along the entire coast of the USA and Canada to Bristol Bay, and the eastern coasts of the Bering Sea (64-65° N lat.).

Callorhinus is one of the six genera of the family of eared seals. This genus consists of only one species, the northern fur seal, *Callorhinus ursinus* (L.), 1758, which inhabits the waters of the USSR and is also found outside these areas.

The economic importance of the northern fur seal is quite substantial. These fur seals provide highly valuable, high-quality, and extremely durable fur, and the cost of these furs is quite high as the number of animals caught is comparatively small. (V.A.)

NORTHERN FUR SEAL¹³*Callorhinus ursinus* (Linnaeus, 1758)

1758. *Phoca ursina*. Linnaeus. Syst. Nat., Ed. X, 1, p. 37. Bering Island.
1792. *Siren cynocephala*. Walbaum. P. Artedi genera piscium . . . p. 360. 155° W long. and 53° N lat. to south of Kad'yak Island (after Schaffer, 1958. V.H.).
- 81 1811. *Phoca nigra*. Pallas. Zoogr. rosso-asiat., 1, p. 107. "Dal'nie Kuril'skie o-va" [Remote Kuril Islands] ("Ex ulterioribus insulis curilicis"). The description is evidently of a young (black) animal.
1828. *Otaria kracheninnikovi*. Lesson. Dict. class. H.N., 13, p. 420. Substitute for *Ursus marinus* G. Steller (1751) = *Phoca ursina* Linnaeus, 1758. Bering Island.
1835. *Phoca mimica*. Tilesius. Oken's Isis, p. 715. Terpeniya Bay, Sakhalin.
1866. *Arctocephalus californianus*. Gray. Catal. of Seals and Whales, Brit. Mus., p. 51. Monterey. California.
1897. *Callorhinus alascanus*. Jordan et Clarck. Fur Seals and Fur-seal Islands, p. 45. Pribilof Islands.
1898. *Callorhinus curilensis*. Jordan et Clarck. Ibid., p. 45. Tyulenii Island, Sakhalin. (V.H.)¹⁴

Diagnosis

Only species of the genus.

Description

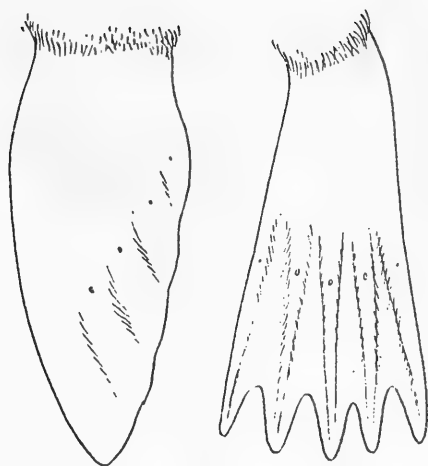
The head is comparatively small, the snout short, pointed, proportional to the width, and the nose not upturned.

The fore and hind flippers are very long, the latter measuring 30% of the body length (Fig. 56).

The guard hairs in the hair coat are longer than the fur hairs. The underfur is more developed in males up to 3-4 years and in females up to 5-6 years, being sparse in much older animals. Thickening of the skin and long hairs on the neck of adult males are distinctly visible features from

¹³ Also known in the Russian language as "Morskoi kot," "kotik," or "kot". Black fur seals are the newborn ones before the first molt; gray fur seals—2 to 3 months after birth; bachelors—young males aged 2 to 5 years; idle (maturing) bulls—males aged 6 to 7 years; bulls—fully mature males older than 7 years; cows—females of all ages.

¹⁴ Synonymy based on the assumption of the systematic identity of all "herds" of the fur seal and data on mixed populations (see "Geographic Variation"). (V.H.)



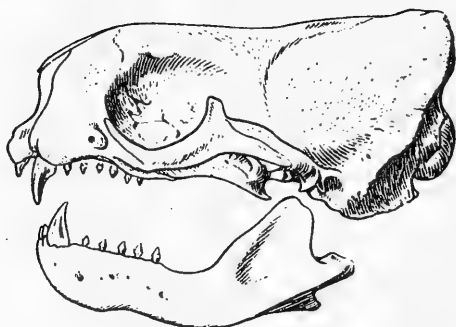
81 Fig. 56. Fore and hind flippers of the fur seal, *Callorhinus ursinus* (figure by N.N. Kondakov).

the age of five years. The whiskers in both sexes are directed downward and long: in males 30-38 cm, in females 20-25 cm.

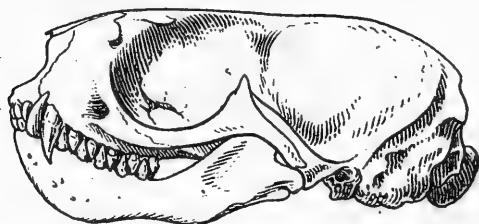
Adult males are monochromatic yellowish-brown, gray or brownish-black, with coloration determined by the color of the guard hair. The anterior part of the snout (around the lips and nose) is grayish-yellow, while the flippers are black. The underfur is not dense and is rusty-brown. The coloration of young males is quite diverse, with a predominance of yellowish-brown and silvery tones. The lower part of the body is lighter in color than the upper. Females are cinnamon-brown, rusty-grayish-yellow around the nose and lips, with dark brown head, nape, back, throat, and upper part of the breast and a very light belly. The flippers are brownish-black. The color of young males resembles that of females. The winter and summer hair coats are identical.

82 The color of the whiskers varies with age. In males and females up to three years of age inclusively, the whiskers are dark, almost black, while in those 4-5 years old, they are dark or light, with some animals sporting dark- and light-colored whiskers. In five-year-old males yellowish-white whiskers predominate. In both sexes of fur seals older than five years, the whiskers are wholly monochromatic, yellowish-white.

The premaxillae are sharply narrowed centrally and highly broadened preapically. The posterior margin of the palatines usually has an acute angle projecting forward. The jaw section bearing molars is comparatively weak (Figs. 57, 58, 59). (For a detailed description of the skull, see above under description of the genus.)



82 Fig. 57. Skull of adult male fur seal, *Callorhinus ursinus* (figure by N.N. Kondakov).



82 Fig. 58. Skull of adult female fur seal, *Callorhinus ursinus* (figure by N.N. Kondakov).

Age-related Average Size (cm) of Male Fur Seals of Tyulen' Island

<i>Age in Years</i>	<i>Size</i>
1	about 95-100
2	from 90 to 112
3	from 103 to 123
4	from 119 to 136
5	from 130 to 150
6 (maturing bulls)	about 175
Adult bulls	about 200

Females 4-5 years old do not exceed 115-120 cm, while adults reach 130 cm or slightly more.

The condylobasal length of the skull in males is 222-241 mm (\bar{x} = 232.3), in females 182-200 mm (\bar{x} = 189); width at the zygoma in males 135-142 mm (\bar{x} = 138.7), in females 111-116 mm (\bar{x} = 114.3); maximum width of skull in males 118-131 mm (\bar{x} = 124.3), in females 94-98 mm (\bar{x} = 96); length of upper row of teeth in males 65-73 mm (\bar{x} = 67.7), in females 50-60 mm (\bar{x} = 54).

Average Weight (kg) of Male
Fur Seals of Tyulen' Island

<i>Age in Years</i>	<i>Weight</i>
1	15-20
2	about 20
3	about 29
4	35-36
5	about 55

The weight of a bull can reach 250 kg.

Average Weight (kg) of Female
Fur Seals of Tyulen' Island

<i>Age in Years</i>	<i>Weight</i>
2	25
(one specimen)	
3	25.6
4	29.1
5	30.7
6	35.5
7	33.0
8	41.0
9	31
(one specimen)	
Older than 10 years	24-45

The weight of large females can reach 60 kg or more.

The weights (in g) of the internal organs recorded for a nine-year-old female (body length 126 cm, weight 45 kg) were: heart 260, lungs 570, liver 1,450, spleen 51, kidneys 220, pancreas 250, and mesenteries 290. The weights (in g) of the internal organs of an eight-year-old male (body length 174 cm, weight 122 kg) were: heart 700, lungs 1,410, liver 4,700, spleen 330, kidneys 528, pancreas 320, and mesenteries 1,540 (Ognev, 1935; Chapskii, 1963; Dorofeev, 1964; A. Sokolov *et al.*, 1969). (V.A.)

Taxonomy

See characteristics of the genus.

Geographic Distribution

This fur seal is predominantly seen in the coastal waters on the western and eastern coasts of the North Pacific Ocean, including the Sea of Japan,



83 Fig. 59. Head of a bull and a female fur seal, Bering Island, July, 1960 (photograph by S.V. Marakov).

the Bering Sea and part of the Sea of Okhotsk. In view of long seasonal migrations the range varies in the course of a year. These fur seals spend the winter months in water in the southern parts of their range and the summer months in the coastal rookeries in the northern parts. The range has not changed significantly from the historic past.

Geographic Range in the USSR

In the summer months the main rookeries of the fur seal are located on Tyulen' Island in the southeastern extremity of Sakhalin in Terpeniya Bay and on the Bering and Mednyi Islands of the Commander group. Small rookeries are seen on two groups of islands (Kamennye Lovushki and Skali Sredneva) of the Kuril range. Individual or small groups of fur seals may be encountered at many points on the coast of the Sea of Japan, on the eastern coast of Sakhalin, on some islands of the Kuril range (Urup, Itirup, etc.), on the eastern coast of Kamchatka right up to Olyutorsk Gulf (60° N lat.), and sometimes even farther north up to the Gulf of Anadyr (Fig. 60).

Fur seals winter outside the USSR waters but some stray animals can be seen close to our coasts. Fur seals wintering in the Sea of Japan

are sometimes seen on Primor'e coasts in the Sea of Japan (at some stray points) and in the waters of the southern Kuril Islands; a few tens of fur seals are often seen in winter in Olyutorsk Gulf and close to the southeastern extremity of Mednyi Island (Commander Islands).

Range outside the USSR (Fig. 61)

One more (the largest) summer rookery of the fur seal is located on the Pribilof Islands (St. Paul and St. George) in Bristol Bay (southeastern part of the Bering Sea). Fur seals move for feeding to the north of these islands (100 miles or more) in summer when large herds can be

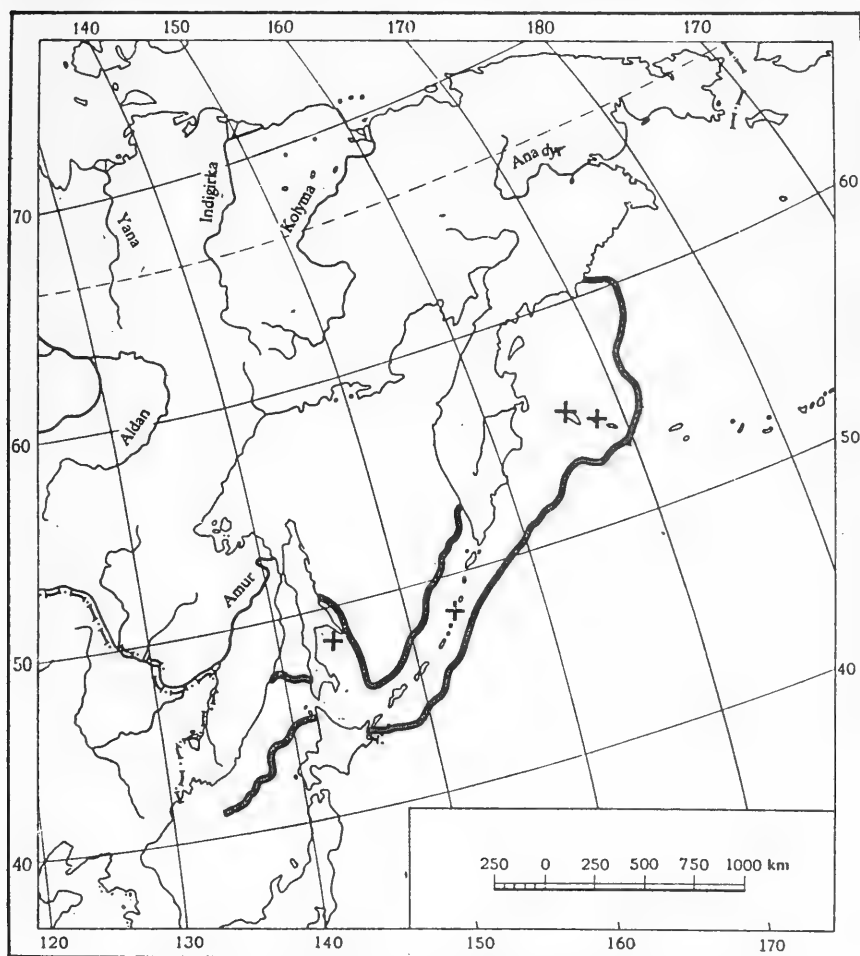


Fig. 60. Range of the northern fur seal, *Callorhinus ursinus*, in the USSR. "+" indicates the sites of summer coastal rookeries (V.A. Arsen'ev).



85 Fig. 61. Range of the fur seal, *Callorhinus ursinus* (V.A. Arsen'ev). 1—Recent finds of the fur seal; 2—coastal rookeries of the fur seal in summer.

seen there. Some move even farther northward, quite often reaching the southern part of the Bering Strait. Simultaneously, they are seen along the entire coast of Canada and that of the USA as far as California.

In the summer of 1965, on the beach of St. Miguel Island in California, some 10 adult fur seals were sighted. In the next two years, 15 to 20 adults and some pups were seen there, and by 1968 the population had increased to about 100 (including newborns). The females included five tagged animals, four from the Pribilof Islands, and one from the Commander Islands with a 1960 tag. The animals lay close to a rookery of California sea lions and some elephant seals (Peterson, Boeuf, and Delong, 1968). This rookery was inhabited in subsequent years also.

Three regions of large winter concentrations of the fur seals are known: the Sea of Japan, the Pacific waters of Japan, and the coastal regions of California. In the Sea of Japan, fur seals are found mostly in the western (Korean Bay) and central parts of the sea in the large Yamato shallow waters (38-40° N lat. and 133-136° E long.). The southern boundary of their extent passes along 36-37° N lat., but they are not found south of it. In the Pacific Ocean wintering herds were seen from the eastern coast of Hokkaido 36-38° N lat. on the coasts of Honshu 150 miles or more away from the coast. In the Californian region the southern boundary of the range passes through 33-34° N lat. but toward the north the wintering area reaches 40° N lat. Some groups could be found in winter over much of the course of the migration route, along the coasts of Washington and Oregon states, in the waters of British Columbia, in the Gulf of Alaska, and even close to the Pribilof Islands in the Bering Sea. (V.A.)

Geographic Variation

The typical variation of fur seals cannot be fully explained by conventional systems. It has long been customary to distinguish three subspecies, which were generally isolated on the basis of their breeding grounds, wintering sites, and migratory routes from summer rookeries to wintering waters (allopatric). While the differences of form are slight and poorly defined, there is nevertheless some exchange of individuals between all the three subspecies, though to an insignificant extent. With increase in population density (overcrowding), this exchange has also increased from year to year.

For these reasons, some authors (Scheffer, 1958; and others) refrain from recognizing distinct morphological geographic variation in this species. This point of view is perhaps justified; however, the geographic isolation of the three groups of fur seals is quite real and this compels

us to recognize three independent populations or stocks of the species. A thorough analysis of the prevailing taxonomic relationships between these populations is therefore necessary.

1. **Commander fur seal**, *C. ursinus ursinus* (Linnaeus, 1758) (syn. *kracheninnikovi*).

The head and neck are relatively more elongated than in the other forms. On the fore and hind flippers, 2-3 underdeveloped claws are visible. The general background color of the young of both sexes is muddy, while the underfur is a rusty-brown.

Summer rookeries are on the Commander Islands and winter sites are in the Sea of Japan and on the islands tending to the Japanese waters of the Pacific Ocean in the south up to 36° N lat., opposite Honshu (Hondo) Island.

2. **Kuril fur seal**, *C. ursinus niger* (Pallas, 1811) (syn. *mimica curilensis*).

The head is broader than that of the Commander fur seal. On the fore flippers 2-3 underdeveloped claws are visible. The underfur is whitish.

Summer rookeries are on Tyulen' Island in Terpeniya Bay (Sakhalin) and winter sites in the Sea of Japan and the Pacific Ocean east of Japan.

87 3. **Pribilov Alaskan fur seal**, *C. ursinus cynocephalus* (Wallbaum, 1792) (syn. *californianus*, *alascanus*).

The head is broadest, compared to the other forms massive, and the neck is thick. Claws are absent on the fore flippers. The general background color of the young fur seal is cinnamonic.

Summer rookeries are seen on the Pribilov Islands in Bristol Bay of the Bering Sea and winter sites in the Pacific waters on the southern coast of the Aleutian archipelago, along the mainland coast of North America, and south up to California (San Diego, around 30° N lat.).

Large-scale tagging of pups was undertaken in the last two decades in all the breeding islands of the fur seal. In some years over 50,000 pups were tagged and these provided voluminous factual information on distribution and migration (Fig. 63). The recovered tags showed that the fur seals of all three populations intermix in the winter areas and also in the coastal rookeries. The extent of mixing of the different populations varies. The population of Tyulen' Island is the most isolated; here the annual recovery of tags exceeded 1,000. Among the fur seals with tags caught here, those with Tyulen' Island tags accounted in some years for up to 97-99%; those with Commander Island tags 0.6-0.9%; and those with Pribilov Island tags 0.3-1.3%. At the same time, in the rookeries



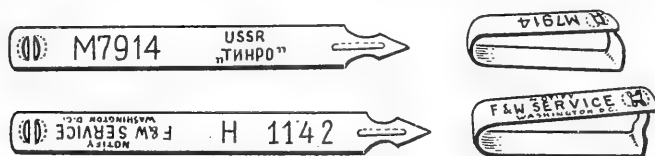
86 Fig. 62. Nostril area of the fur seal, *Callorhinus ursinus* (figure by N.N. Kondakov).

on Tyulen' Island females with Pribilov tags were seen every year. These gave birth there and suckled the pups. The age of some of them, as determined from the tag number, exceeded 10 years.

The fur seals of Tyulen' Island are comparatively isolated even in the winter areas in the Sea of Japan. In 1963-1965, of 49 tagged animals caught, 42 were of the Tyulen' Island seals, four of the Commander, and three of the Pribilov Islands (Arsen'ev, 1964).

Fur seals from Tyulen' Island mix to a large extent with those of other populations while wintering in the Pacific waters of Japan. Here, in 1961-1965, of 566 tagged animals recovered, 376 (66.8%) were of Tyulen' origin, 121 (21.6%) of Commander origin, and 66 (11.6%) of Pribilov origin. Three had tags of the Kuril Islands.

Mixing of the fur seals on the Commander Islands is far greater than on Tyulen'. Among the tagged fur seals, about 10% had Pribilov tags and less than 1% Tyulen' tags. It is interesting to note that on Mednyi Island,



87 Fig. 63. Tags for marking the fur seal: Russian tags on top and American tags below.

more fur seals with Pribilov tags were recovered than those with tags of the adjoining Bering Island.

The population of the Pribilov is very poorly supplemented with fur seals from the western part of the Pacific Ocean. Among 5,000-6,000 tagged fur seals, not more than 20-40 were "aliens". There is no doubt that the Pribilov population, at least ten times larger than any other population, is of great importance.

The recovery of tagged fur seals on the Kuril Islands showed that the stock here is supplemented equally by all the populations of fur seals. (V.A. and V.H.)

Biology

Population. The population of fur seals is determined in the summer rookeries on the beaches, where a good proportion of each population gathers. The population of the Commander Islands is about 200,000, Tyulen' Island 160,000 - 170,000, and the restored population of the Kuril Islands is roughly 15,000. The largest population, close to 2 million, is the Alaskan one on the Pribilov Islands. The total population of fur seals in the northern parts of the Pacific Ocean is thus roughly 2.5 million.

Habitat. In winter and spring, for approximately six months, the fur seals live scattered in the open sea and form no sizable herds. In summer they form large coastal herds on the same islands every year.

Rookeries are of different types: in some cases these are purely sandy or pebbled beaches at the foot of a cliff (Tyulen' Island and the main harem on Mednyi Island); others are rocky platforms with scattered large boulders (northern rookery on Bering Island); some other rookeries are wholly covered by massive rocks with no level surface. Fur seals need a typical protective belt, most often in the form of underwater reefs or boulders projecting above the water which serve as good breakwaters and protect the rookery from storm waves. In the quiet zone thus formed pups learn to swim. Sometimes huge shallow waters in front of the rookery serve as protection. Many rookeries are characterized by massive thickets of seaweeds (Voloshinov, 1889; Grebnitskii, 1902; Suvorov, 1912; Tikhenko, 1914).

Food. Newborns grow up on the mother's milk for the first four months of life in the coastal rookeries (up to October or November) (Fig. 68). With the changeover to a marine mode of life, they begin to feed on the same food as consumed by adults.

The stomachs of fur seals caught in the coastal rookeries were usually empty. Only some of them (under favorable conditions) revealed food remnants, generally in the form of small bits of fish or cephalopods. This

information is not adequate for characterizing the food of fur seals in the coastal rookeries (Kenyon, 1956). Therefore, the information on the food of fur seals in the different parts of the range characterizes their food when living at sea.

Among the fur seals caught in the sea throughout the range of the species, many stomachs were empty. In the western part of the Pacific Ocean the number of empty stomachs varied from 22 to 84% (average 45%) of those examined, and in the eastern part 31 to 63% (average 45%).

In the western part of the Pacific Ocean, the fur seals feed on 21 species of fish and 10 species of cephalopods (in some cases fish or cephalopods were identified only to the level of genus or family). The number of species of animals consumed by the fur seals in the eastern part of the Pacific Ocean was considerably higher. Here 48 species of fish and six of cephalopods were identified as food of the fur seals.

In the western part of the Pacific Ocean in the region of the Commander Islands, sand eel and greenling serve as the main food, and in the Sea of Okhotsk (southeastern part), Alaska pollock, greenling, and some species of squids. In the Pacific waters of Japan most stomachs contained lantern-fish although two species of squids were quite common. In the western part of the Sea of Japan (Korean Bay), Alaska pollock is the almost exclusive food (in some, 99% of it) while in the central part of the sea (Yamato coast) the squid *Gonatus magister* serves as the predominant food (Table 6).

90 In the eastern part of the Pacific Ocean, in the Californian region, the most important food items are hake followed by anchovy, saury, and two species of squids; along the Oregon and Washington coasts, hake and sand eel, and to a small extent herring, capelin, sea perch, and squid; and on the Alaskan Peninsula sand eel and capelin followed by herring and squid. Prime fishes comprise the main food items only in some regions and the prevailing view about the damage caused by fur seals to Alaskan fisheries is clearly an exaggeration. Seasonal changes in food have not been adequately studied (Taylor *et al.*, 1955; Scheffer, 1950a*; Kenyon, 1956; Wilke and Kenyon, 1957; Arsen'ev and Fedorov, 1964; Pike, 1964, 1966a*) (Table 7).

The average daily food requirements of fur seals in Pacific waters is 1,700 g and in the Sea of Japan 2,500 g, depending on the calorific value of food (anchovy, mackerel, and squid in the former case and Alaskan pollock in the latter) (Panina, 1966). The maximum weight of the stomach contents of large males is 10 kg (17 kg in one case), of adult females 2.5 to 3 kg.

89 Table 6. Food of the fur seal in the western part of the Pacific Ocean (Arsen'ev and Fedorov, 1964)

Pacific waters of Japan	Sea of Japan	Sea of Okhotsk	Bering Sea, region of Commander Islands
1	2	3	4
Fishes	Fishes	Fishes	Fishes
Headlight fish, <i>Diaphus</i> sp.	Pacific salmon, <i>Oncorhynchus</i> sp.	Japanese anchovy, <i>Engraulis japonicus</i>	Pacific salmon, <i>Oncorhynchus</i> sp.
Gissu, <i>Pterothrissus gissu</i>	Humpback salmon, <i>Oncorhynchus gorbuscha</i>	Pacific salmon, <i>Oncorhynchus</i> sp.	Humpback salmon, <i>Oncorhynchus gorbuscha</i>
Sardine, <i>Sardinops melanosticta</i>	Alaska pollock, <i>Theragra chalcogramma</i>	Humpback salmon, <i>Oncorhynchus gorbuscha</i>	Alaska pollock, <i>Theragra chalcogramma</i>
Japanese anchovy, <i>Engraulis japonicus</i>	Atka mackerel, <i>Pleurogrammus monopterygius</i>	Pacific herring, <i>Clupea harengus pallasii</i>	Char, <i>Salvelinus</i> sp.
Pacific salmon, <i>Oncorhynchus</i> sp.	Asian greenling, <i>Pleurogrammus azonus</i>	Lantern fishes, Myctophidae	Atka mackerel, <i>Pleurogrammus monopterygius</i>
Humpback salmon, <i>Oncorhynchus gorbuscha</i>	Sand fishes, Trichodontidae	Pacific saury, <i>Cololabis saira</i>	Pacific sand lawce, <i>Ammodytes hexapterus</i>
Lantern fishes, Myctophidae	Cephalopoda	Alaska pollock, <i>Theragra chalcogramma</i>	Smooth lumpsucker, <i>Aptocyclus ventriosus</i>
Lantern fish, <i>Scopelarchus linguidens</i>	Squids	Greenling, <i>Pleurogrammus</i> sp.	Greenland halibut, <i>Reinhardtius hippoglossoides</i>
Lantern fish, <i>Myctophum californiense</i>	<i>Watasenia scintillans</i>	Asian greenling, <i>Pleurogrammus azonus</i>	Cephalopoda
Anchovy, <i>Notoscopelus elongatus</i>	<i>Gonatus fabricii</i>	Cephalopoda	Squids
	<i>Gonatus magister</i>		<i>Gonatus fabricii</i>
	<i>Ommatostrephes sloanipacificus</i>	Squids	<i>Gonatus magister</i>
Pacific saury, <i>Cololabis saira</i>		<i>Gonatus</i> sp.	

Contd.

1	2	3	4
Lantern fish, <i>Electrona</i> sp.		<i>Gonatus fabricii</i> <i>Gonatus magister</i>	
Barracuda, <i>Sphyræna</i> sp.		<i>Gonatopsis</i> <i>borealis</i>	
Pacific cod, <i>Gadus macrocephalus</i>		<i>Ommatostrephes</i> <i>sloani-pacificus</i>	
Alaska pollock, <i>Theragra chalcogramma</i>			
Pacific mackerel, <i>Scomber japonicus</i>			
Japanese horse mackerel, <i>Trachurus</i> <i>japonicus</i>			
Prometheus fish, <i>Promethichys prometheus</i>			
Mackerel, <i>Pneumatophorus japonicus</i>			
Cephalopoda			
Octopoda			
<i>Polypus vulgaris</i>			
Squids			
<i>Loligo bleekeri</i>			
<i>Onychoteuthis banksii</i>			
<i>Moroteuthis bonnbergii</i>			
<i>Watasenia scintillans</i>			
<i>Gonatus fabricii</i>			
<i>Gonatus magister</i>			
<i>Chiroteuthis veranyi</i>			
<i>Ommatostrephes</i> <i>sloani-pacificus</i>			

The fur seals held in an oceanarium at Enosima (Japan) were fed mainly squids. The animals were given as much as they could consume, which averaged 3 to 7 kg. Seals of 2-5 years of age consumed 3-4 kg and those of 6-9 years 5-7 kg. Experiments with two and three feeds showed

91 Table 7. Food of the fur seal in the eastern part of the Pacific Ocean (Arsen'ev and Fedorov, 1964)

California	Oregon, Washington, and British Columbia	Gulf of Alaska and Bering Sea
Fishes	Fishes	Fishes
<i>Lampetra tridentata</i>	<i>Lampetra tridentata</i>	<i>Lampetra tridentata</i>
<i>Squalus acanthias</i>	<i>Hydrolagus collici</i>	<i>Clupea harengus pallasii</i>
<i>Alosa sapidissima</i>	<i>Alosa sapidissima</i>	<i>Oncorhynchus</i> sp.
<i>Clupea harengus pallasii</i>	<i>Clupea harengus pallasii</i>	<i>Oncorhynchus gorbuscha</i>
<i>Engraulis mordax</i>	<i>Engraulis mordax</i>	<i>Oncorhynchus keta</i>
<i>Oncorhynchus</i> sp.	<i>Oncorhynchus</i> sp.	<i>Oncorhynchus kisutch</i>
<i>Hypomesus pretiosus</i>	<i>Oncorhynchus gorbuscha</i>	<i>Oncorhynchus nerka</i>
<i>Thaleichthys pacificus</i>	<i>Oncorhynchus kisutch</i>	<i>Oncorhynchus tshawytscha</i>
<i>Tactostoma macropus</i>	<i>Oncorhynchus nerka</i>	<i>Mallotus villosus</i>
<i>Magnisudus baryosoma</i>	<i>Oncorhynchus tshawytscha</i>	<i>Thaleichthys pacificus</i>
Myctophidae	<i>Salmo gairdneri</i>	<i>Lampanyctus nannochir</i>
<i>Tarletonbania crenularis</i>	<i>Hypomesus pretiosus</i>	<i>Anotopterus pharap</i>
<i>Cololabis saira</i>	<i>Mallotus villosus</i>	<i>Microgadus proximus</i>
<i>Merluccius productus</i>	<i>Thaleichthys pacificus</i>	<i>Theragra chalcogramma</i>
<i>Syngnathus californiensis</i>	<i>Scopelosaurus</i>	<i>Gasterosteus aculeatus</i>
<i>Trachipterus trachipterus</i>	Myctophidae	<i>Sebastodes</i> sp.
<i>Trachurus symmetricus</i>	<i>Tarletonbania crenularis</i>	<i>Sebastodes alutus</i>
<i>Brama rayi</i>	<i>Cololabis saira</i>	<i>Anoplopoma fimbria</i>
<i>Medialuna californiensis</i>	<i>Gadus macrocephalus</i>	<i>Pleurogrammus monopterygus</i>
<i>Scomber japonicus</i>	<i>Merluccius productus</i>	<i>Reinhardtius hippoglossoides</i>
<i>Sebastodes</i> sp.	<i>Microgadus proximus</i>	<i>Aptocyclus ventricosus</i>
<i>Sebastodes jordani</i>	<i>Theragra chalcogramma</i>	<i>Trichodon trichodon</i>
<i>Anaplopoma fimbria</i>	<i>Gasterosteus aculeatus</i>	<i>Ammodytes hexapterus</i>
<i>Atherinopsis californiensis</i>	<i>Trachipterus trachipterus</i>	<i>Bathymaster signatus</i>
<i>Citharidithus</i> sp.	<i>Trachurus symmetricus</i>	<i>Anarhichas orientalis</i>
<i>Liopsetta exilis</i>	<i>Brama rayi</i>	<i>Atheresthes stomais</i>
<i>Polichthys notatus</i>	<i>Sebastodes</i> sp.	<i>Hippoglossus stenolepis</i>
Cephalopoda	<i>Sebastodes eumelas</i>	Cephalopoda
<i>Tremoctopus</i> sp.	<i>Anaplopoma fimbria</i>	<i>Loligo opalescens</i>
<i>Loligo opalescens</i>	<i>Ammodytes hexapterus</i>	<i>Gonatus</i> sp.
<i>Onychoteuthis</i> sp.	<i>Tetragonurus cavi</i>	<i>Gonatus fabricii</i>
<i>Onychoteuthis banksii</i>	<i>Atheresthes stomais</i>	<i>Gonatus magister</i>
<i>Abrialopsis</i> sp.	<i>Liopsetta exilis</i>	<i>Gonatopsis</i> sp.
<i>Gonatus fabricii</i>	Cephalopoda	<i>Gonatopsis borealis</i>
<i>Gonatus magister</i>	<i>Loligo opalescens</i>	Other mollusks
<i>Gonatopsis borealis</i>	<i>Onychoteuthis</i> sp.	
<i>Dosidicus gigas</i>	<i>Onychoteuthis banksii</i>	
<i>Moroteuthis robusta</i>	<i>Gonatus</i> sp.	
	<i>Gonatus fabricii</i>	
	<i>Gonatus magister</i>	
	<i>Gonatopsis borealis</i>	

that the intake was practically identical in both cases. They consumed more food in summer than in winter. The food intake by the various age groups varied from 8 to 22% of the body weight, on average 10% (Nakajima, Sawaura, and Oda, 1963).

Some tens of cases are known of the presence of various species of marine bird remnants in the stomach of fur seals; these are obviously cases of incidental intake.

Home range. Harems covering 10 m² or more represent definite sections of habitation on the coasts. The site for a harem is selected and protected by the bull, who arrives first (see under "Daily Activity and Behavior"). With the disbanding of the harems, these isolated sections disappear. The young animals live on the fringes of harems and have no specific section in the rookery.

Daily activity and behavior. Fur seals living on the beaches are more active in the day and there is continuous movement among the animals. They are quieter at night, with feeding apparently confined to the early morning hours.

While at sea, the feeding regime shows certain regional features. In the Sea of Japan, fur seals begin active feeding in the predawn hours, which decreases toward midday. Between 1:00 and 4:00 p.m. the seals rest, mostly on the water surface, and then set out for the second round of active search; the time of feeding termination has not been established (Panina, 1964). In the Pacific waters of Japan, in winter-spring, only a single period of active search has been observed—from predawn to mid-day. By 6:00 - 8:00 p.m. most of the stomachs are already empty (Panina, 1966a). These differences are the results of the varying accessibility of food during the day in a given region of habitation.

The behavior of fur seals of different age and sex groups differs at sea and in the coastal rookeries. In spring, in the latter half of May, bulls are the first to arrive in any region of the range and occupy a small section on the vacant beach (Fig. 64). No consideration is apparently given to the convenience of the location of the future harem when selecting the site. Possibly, many bulls attempt to occupy those sections in which they spent the previous year (Kenyon, 1960). The bulls fight savagely with
91 their competitors to assert their right over territory, inflicting serious wounds on each other during such battles. Usually the bulls arrange themselves at a distance of 2-5 m from each other. During this period there is frequent change of bulls in the sections because the stronger ones arriving later drive away the weaker occupants. In such cases, however, the new arrival has invariably to reckon with two or three neighboring males, so that even a very strong latecomer is not always successful in entrenching himself in the rookery.



92 Fig. 64. Formation of a fur seal rookery: bulls have occupied territories for their harems. Bering Island, June, 1962 (photograph by S.V. Marakov).

After the bulls, usually from early June, immature males (bachelors) begin to arrive. The first to appear are the four-to-five-year-olds, followed by three-year-olds at the end of June, and two-year-olds from mid-July; year-old males arrive only in August or even in September. A small number of bachelors of all ages can be seen throughout the summer. These
 94 bachelors live along the fringes of the harems, forming a dense inactive zone; but some bachelors move quite freely in a harem section before the arrival of a female. At this time, bulls pay them little heed while the appearance of a new bull invariably invites hostilities. In clear weather bachelors visit the sea during the day but remain close to the rookery and return at night for rest. In cloudy and foggy weather they spend most of the day in the rookery, often playfully imitating the brawls of bulls.

The first of the females arrive in the first ten days of June (Fig. 65) and their arrival en masse commences in the second half of June or even in early July. Females in the last stages of gestation arrive singly, more rarely in small groups. Bulls do not influence the females during harem selection, leaving the choice entirely to them. Quite often, females move freely from one group to another and only sometimes does a bull prevent a female from leaving his harem, even using force if necessary.



92 Fig. 65. Formation of the first harem. Tyulen' Island, June, 1968 (photograph by V.A. Arsen'ev).

He grasps the skin of the escapes with his teeth and throws her back into the harem. Upon arrival on the beach the females join more enthusiastically the groups already formed rather than single bulls. With the commencement of the large-scale (Fig. 66) arrival of females, the harems gradually enlarge and merge, forming collective harems whose boundaries are difficult to demarcate. At the peak of harem life the rookery represents a densely packed mass of females with bulls scattered among them (Fig. 67). With the arrival of females, the bulls drive the bachelors away from the harem area.

When moving on land, some fur seals put forward one of the fore flippers, draw up both the hind flippers simultaneously and then, in the same sequence, bring forward the other fore flipper and pull up the two hind flippers. Alternatively, both fore flippers are directed forward simultaneously and the body weight is shifted onto them before dragging both hind flippers forward with a jerk. Such a mode of locomotion resembles short hops and the animal moves more rapidly in this manner (Mordvinov, 1968). Usually, fur seals move very slowly. But it is difficult for a running man to catch an animal intent on distancing itself (for a short distance).

Females undergo parturition soon after arrival in the rookery. The time between arrival and parturition varies from 2 to 99 hr (average 22 hr). The female on arrival on the coast, sleeps much of the time before parturition. The bull protects more attentively a female that has



93 Fig. 66. Increasing number of harems. Mednyi Island, June, 1969 (photograph by S.V. Marakov).

delivered and does not allow her to leave his harem because mating commences soon after parturition. The interval between parturition and mating varies from two to seven days (average four days). During this period the females are confined to the rookery and suckle the pups (Fig. 68) but go to the sea for feeding soon after fertilization (Bychkov, 1964b). On leaving the rookery for the first time, the female stays at sea for about a week; on returning, she quite easily finds her own pup among the thousands present (Fig. 69). The females suckle only their pups and do not entertain others. The periodicity of subsequent departures to the sea and return to the beach cannot be tracked in such a massive gathering of animals.

Marking the Tyulen' Island bulls with a quick-drying paint showed that not a single male remains in the rookery for the entire harem period; rather, there is a continuous exchange of bulls. Of the 54 marked bulls, 57% stayed continuously for 1 to 15 days, 26% for 16 to 30 days, and 17% for over a month. In this period, however, all of them went out to sea several times, returning to the rookery thereafter. None of the bulls spent more than a week in the rookery without going out to sea. Most often, the bull left for a brief period and, having been invigorated at



93 Fig. 67. Nearly full rookery. Some bulls still without harems. Mednyi Island, end of June, 1969 (photograph by S.V. Marakov).



95 Fig. 68. Female fur seal suckling a pup. Mednyi Island (photograph by S.V. Marakov).



95 Fig. 69. Harem females returning to the beach after being out to sea on a warm day. In the background are haremless bulls. Tyulen' Island, June, 1966 (photograph by V.P. Popov).

sea, returned to his place. The main reasons for going out to sea are a rise in the ambient temperature or fright, but in some cases sea outings were prompted for no apparent reason. Along with brief absences, there were also prolonged departures of marked bulls to the bachelor quarters where the bulls rested peacefully shoulder to shoulder with the bachelors and other bulls. Some of them returned to the harem after a few days and exhibited their prowess. The bull rarely finds his old place since three or even four bulls press him, compelling him to leave (Fig. 70). It is for this reason that some marked bulls were noticed at different times in six or seven different sections of the rookery (Bychkov and Dorofeev, 1962; Dorofeev and Bychkov, 1964). Evidently the bulls arriving first and occupying a site farthest from the coast can remain the longest in their territory (average 54.4 days) compared to those who come later and set up a harem along the coast (average 34.2 days). However, the former can hold a harem together only for a very short interval (average 19.1 days) compared to the latter (27.2 days) (Kenyon, 1960).

96 Immediately after birth, the pups lie alongside their mothers for the first few days (Fig. 71) and, after her departure, gather in groups forming a nursery farthest from the sea coast. At this time they sleep soundly for



96 Fig. 70. Bulls barring the entry of a competitor into the rookery (in the foreground). Tyulen' Island, June, 1968 (photograph by V.A. Arsen'ev).



96 Fig. 71. Fur seal pup ("black pup"). Bering Island, July, 1969 (photograph by S.V. Marakov).

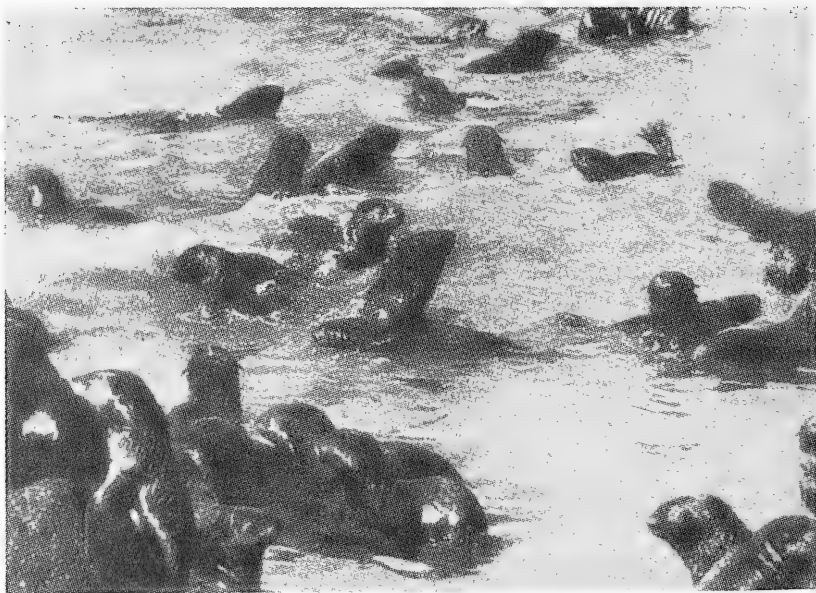
most of the time and do not feed for the six or seven days their mothers are out to sea. Later, the pups are fed at intervals. In the event of a mother's death, her pup inevitably dies of starvation since none of the thousand or more other mothers in the rookery will take in a stranger. The growing pups move throughout the rookery beyond their harems,

sleep much, and often play with each other for long periods. Later, they learn to swim (Fig. 72), after which they spend considerable time at sea in fair weather.

Pups are capable of independent movement on land almost
97 immediately after birth and those that have grown strong move long distances throughout the rookery, mostly resorting to short hops. Their speed is such that a man walking rapidly could keep pace.

With the disbanding of the harems, the division of the rookery into age and sex groups ceases. Bachelors move freely and bulls and females fill the bachelor quarters, pups are seen everywhere, brawls cease, and bulls lie quietly beside bachelors and maturing bulls. By October the fur seals of all the coastal rookeries begin leaving for the sea. The animal population dwindles and by the end of November the coast is deserted.

Once in water, the animals become agile and quick. In the usual method of swimming the seals use the fore flippers as the main locomotor organs and can also use them as rudders or brakes. For a comparatively small distance the hind flippers can also fulfill the role of a locomotor organ but usually they serve as rudders and stabilizers. In rectilinear motion the hind flippers are stretched out along the longitudinal [longer] axis of the body and set vertically. The fore flippers are first deflected



97 Fig. 72. Pups learning to swim at the coast. Bering Island (photograph by S.V. Marakov).

forward and raised upward at an angle and then moved backward before ultimately being pressed to the trunk. In the last stage of this process the movement of the fore flippers can be very sharp so that it generates the great thrust necessary for the animal to jump high above the water. Quite often a herd is seen swimming rapidly by resorting to high long jumps above the water ["porpoising"] but such maneuvers are used to cover only very short distances.

A fur seal, swimming steadily, can cover 5-6 miles an hour. When resorting to jumps, the speed rises to eight miles or more (Mordvinov, 1968).

98 Most fur seals return annually to the same ground where they were born. The migration of some to other populations hardly disturbs this pattern. The fur seals return to their own island even when the islands are situated close to each other, for example: Bering and Mednyi Islands (the Commanders), and St. Paul and St. George (the Pribilofs) (Nagasaki and Matsumoto, 1957; Arsen'ev and Fedorov, 1964; Chugunkov, 1966).

Seasonal migrations and transgressions. The distances of seasonal migrations of the northern fur seal, which reach 1,200-3,500 km, are the longest among the pinnipeds. Autumn migrations commence at the end of October to November. The animals set out singly or in small groups. First to leave are the adult males, followed by the much younger females and males. Old females and three-to-four-month-old gray pups stay the longest in the rookery. Each of these three groups follows its own migration route, the study of which is largely based on an analysis of the tags recovered.

The Kuril seals, inhabiting Tyulen' Island in summer, almost invariably take one of just two migratory routes. A part of the population enters the Sea of Japan through La Perouse Strait, where they winter. Another part enters the Pacific waters through the southern Kuril Strait and, moving southward, disperses along the eastern coasts of Hokkaido and Honshu islands. Many seals probably cross Sangarsk Strait in December-January into the Sea of Japan and join those which have arrived there from the north.

In winter months the disposition of fur seals in the Sea of Japan is determined by the availability of food and the hydrologic conditions. The bulk of them inhabit two regions of the sea: the western part from Peter the Great Gulf to the Korean Bay and the central part in the region of Yamato coast (38-40° N lat.). The older bulls apparently do not cross south of 42° N lat. In the waters between these two regions only stray fur seals are encountered.

The return journey from the Korean Bay commences in March and is greatly intensified in April. The fur seals move northeast along the

west coast and reach La Perouse Bay in May. By this time, they have already deserted the Korean Bay.

In the central part of the Sea of Japan the fur seals remain throughout April. Some of them move north, joining the migratory course from the Korean Bay in the region of Cape Povorotnyi, while others leave through Sangarsk Strait from where, together with the animals that have wintered in the Pacific Ocean, they move along the Japanese island coasts toward Kuril Strait.

In addition to food, another vital factor determining the winter distribution of fur seals is the surface temperature of the sea. In the Sea of Japan fur seals are encountered in the temperature range -0.6 to $+12^{\circ}$ but prefer not to go beyond 7 or 8°C . The southern boundary of the winter habitat of fur seals is the line of convergence of the surfaces of the much colder Sea of Japan and the very warm Pacific Ocean water bodies, i.e., the line of the "polar front". The northward advancement of this line also compels the seal herds to move northward (K.I. Panin).

In the Pacific waters of Japan fur seals are seen in December and, moving along the coasts of Hokkaido and Honshu islands, reach 38° N lat. and, in some years, even 36° N lat. In February and March the seals are widely distributed between 38° and 40° N lat., away from the coasts on average up to 145° E long. Some can be encountered far more eastward, at 160 to 175° E long. (Birman, 1966). The distribution of animals is not even; they form very dense herds at some places over an extensive area. However, even at these places the seals live in isolation or in small herds.

The hydrologic regime of the eastern coast of Japan is determined by the interaction of two massive currents: the very warm KuroShio and the much colder OyaShio. The zone of convergence of the currents changes with the seasons and thus the distribution of seals changes correspondingly; the animals are confined mainly to the zone where the cold and 99 warm water bodies mix. Food is abundant in this zone. The temperature of surface waters in the regions of habitat of the fur seal varies from 0 to 15°C but the animal is seen more often at temperatures of 6 to 11°C .

In the fur seal herds in coastal waters, males predominate over females in all age groups; this predominance is accentuated with age. In regions far removed from the coasts such a phenomenon is seen only in groups of yearlings; females predominate in all other age groups.

The northward journey of the fur seals commences in April; by May they abandon the southern wintering regions and concentrate in June mainly along the coasts of Hokkaido Island. Later, practically all the fur seals migrate to the summer rookeries on Tyulen', the Kuril, and

the Commander islands. In 55% cases the fur seals migrate individually, in 24% in twos, in 9% in threes, and in 4% in fours. In 8% cases, groups of 5 to 25 seals were seen. In all the age groups up to five years, males migrated earlier than females; among males the much older ones migrated earlier than the younger ones, but this difference in time was very insignificant (Taylor, Fujinaga, and Wilke, 1955).

Females predominate in the winter herds of fur seals in the Sea of Japan (since hunting eliminates only males and the females in the population are usually more numerous). A large number of females are older than 10 years and females of other age groups are roughly in equal proportion but in small numbers. Most males are young, 3-6 years of age. The much older males winter more northward and the one- and two-year-olds almost never enter the Sea of Japan. In the Pacific waters where, too, the females are generally more numerous than the males, the females of all age groups are in equal proportion; unlike in the Sea of Japan, old females do not predominate here. Among males, young ones, including yearlings, are more numerous. The fur seals of all three populations winter in the Pacific waters, though a good part of them are the fur seals of Tyulen' Island.

According to earlier schemes, the fur seals of the Commander Islands migrate (Suvorov, 1912; Boitsov, 1934; Ognev, 1935; and others) along the Kuril range to the eastern coast of Japan, where they winter, and return in spring by the same route to the Commander Islands. An analysis of the large number of tags recovered did not confirm this route since, in this region, the Commander seals constitute a very insignificant proportion of the wintering herd. The wintering regions and the migration routes of the Commander seals have not been clearly ascertained to date.

A very small number of seals is present in winter every year on the southeastern tip of Mednyi Island. In November-December, some are encountered in Olyutorsk Gulf, even in the region of ice floes (Chugunkov and Prokhorov, 1966).

The migration of Alaskan seals also begins in October-November, when they abandon the Pribilof Islands. The autumn migrations occur rapidly in early December and the first seals are already sighted in California at this time. The maximum number of animals winter there in early February. In this period old females predominate; those older than 10 years occupy the southern part of the winter station (up to 33° N lat.); seven-eight-year-old females remain slightly more northward. The males and young (one- and two-year-old) females are rarely seen. Immature females arrive later, their maximum number being seen in the second half of March.

The bulk of yearlings of both sexes winter in the coastal waters of British Columbia and Washington state, where they occupy the well-protected straits and bays. Some seals of 3-4 years of age winter there but do not venture more southward. Most of the yearlings and some of the two- and three-year-olds remain in these regions throughout the year and evidently do not return to the summer rookeries.

100 Migrations are shortest among bulls, which winter in the Gulf of Alaska and partly in the southeastern part of the Bering Sea. This age group is the first to arrive on the Pribilof Islands, from April end to May.

During March most adult females of the Pribilof population leave the southern wintering regions. Young females arriving there later remain longer, usually until the latter half of April. At March end to April old females are seen in the region of Vancouver Island. They move gradually northward and are replaced by younger ones, and by May end to early June almost all the animals found here are under 5 years of age. In May and June congregations of the fur seal are noticed in the Gulf of Alaska and by mid-June mature females and young males reach the Pribilof Islands. Young females join them later and the fur seal population in the Bering Sea reaches its peak in July, August, and September.

Some fur seals (mainly, perhaps, old males) are found in the Pribilof Islands even in the winter months. Males with Pribilof tags have been caught even in Olyutorsk Gulf. A small number of fur seals of both sexes, but of different ages (mostly young), are seen in winter and summer in all the areas of their long migratory route (Kenyon and Wilke, 1953; Taylor *et al.*, 1955; Arsen'ev and Fedorov, 1964; Spalding, 1964a).

Information on the transgressions of fur seals is very scant. At the end of October, 1947, in Nogaev Bay (northern coast of the Sea of Okhotsk), a fur seal was killed and some 20 more were sighted there (Khmelin, 1950). In September, 1958, one was found in the northeastern part of the Sea of Okhotsk (Shelikhov Gulf), three strays in the region of Tauisk Bay, and a group of three close to Okhotsk. The animals were not large, evidently young, and were spotted 1,000 km away from the summer rookeries (Tikhomirov, 1964a). In 1959, three solitary seals were noticed in Gulf of Anadyr (62-63° N lat.) and one was killed in the southern part of the Bering Strait (64° N lat.). All of them were large males, perhaps of the Pribilof population (V.A. Arsen'ev).

Reproduction. In the breeding season, harems of varying strengths are formed in the coastal rookeries. The most favorable ratio is 40-50 females to a bull. The harem population depends mostly on their disposition. Harems close to the sea are usually more populous. On St. Paul

Island the average population of 20 harems was 39 females. Instances are known of a harem comprising as many as 250 females (Boitsov, 1934; Bartholomew and Hoel, 1953). In such cases there was, perhaps, a frequent change of bulls. As harem life reaches peak activity the harem boundaries merge and it becomes difficult to count the females under each bull. While enumerating the number of heads in a herd, the bull-to-female ratio is taken as 1:40-50.

The period of parturition and mating extends for about two months. The first of the newborns are usually found in the rookeries on Tyulen' and the Commander Islands seldom earlier than June 10. The number of pups increases quite rapidly but maximum whelping occurs in the second half of July, after which it begins to taper off. Some births and mating are observed in the first ten days of August, though exceptions do occur somewhat later. Because of the impregnation of the female soon after parturition, gestation is believed to extend to about 360 days. Mating mostly occurs on land, more rarely in shallow water, and can last from 5 to 40 min.

Young females arrive in the harem toward the end of the harem period. On Tyulen' Island four-year-old females (age determined from recovered tags) begin to be seen in the latter half of July and some of them are impregnated. Two-year-old females have not been recorded in the harems before July 25 (Bychkov, 1964a).



101 Fig. 73. A group of "black" pups. Tyulen' Island, July, 1968 (photograph by V.A. Arsen'ev).

101 The male-to-female ratio among newborns is close to 1:1. Of the 4,276 embryos examined during investigations at sea in 1958-1961 in the eastern part of the Pacific Ocean, 2,135 (49.9%) were males and 2,141 (50.1%) females. In the western part of the Pacific Ocean, of the 2,741 embryos examined, 1,393 (50.8%) were males and 1,348 (49.2%) females (Arsen'ev and Fedorov, 1964).

The female usually gives birth to a single pup; twins are extremely rare. In most cases, parturition is annual and sterility comparatively low, but increases in old females. Under the conditions prohibiting the shooting of females and normal herd growth, the annual increment of population was 8-8.5% (Dorofeev, 1964).

Table 8 gives an idea of the number of gestating females according to age. Females in the eastern part of the Pacific Ocean begin reproducing a year later than those in the western part (reason not established).

The period of latent growth of the embryo evidently extends over two months. The embryo grows quite rapidly, and even at this stage the growth of males surpasses that of females, as can be seen from Table 9.

102 *Growth, development, and molt.* The body length of newborns is 60-70 cm and their average weight is 5-6 kg. In individual cases the weight of the newborns may exceed 10 kg. Within a few hours of birth,

101 Table 8. Age-related gestating females (Arsen'ev and Fedorov, 1964)

Age, years	No. of females in sample	Gestating among them	
		Number	Percent
Western part of Pacific Ocean			
4	847	413	53
5	637	531	83
6	423	358	85
7	241	216	90
8	137	125	91
9	94	86	91
10	69	61	88
10+	279	201	72
Eastern part of Pacific Ocean			
4	375	16	4
5	403	180	45
6	445	340	76
7	545	434	80
8	609	519	85
9	555	501	90
10	513	455	89
10+	2,641	2,171	82

102 Table 9. Change in length and weight of embryos in Japanese waters (Arsen'ev and Fedorov, 1964)

Month	Length, cm			
	Males		Females	
	Number in sample	Average length	Number in sample	Average length
February	5	27.0	12	13.2
March	17	33.6	3	31.2
April	151	43.9	146	42.2
May	125	51.5	116	50.8
June	18	57.0	24	53.9

Month	Weight, kg			
	Males		Females	
	Number in sample	Average weight	Number in sample	Average weight
February	1	0.4	6	0.1
March	17	1.3	3	0.8
April	151	2.1	146	1.9
May	125	3.7	116	3.3
June	18	6.2	24	4.8

pups begin moving quite freely throughout the rookery. They gather strength quickly and, after a few days of suckling, form separate groups, mostly away from the sea. The stomach volume of a newborn pup weighing 4.5 kg was 1.1 liter, and of another 1 liter (fat content of seal milk about 45%). After 3-4 months, by the end of the suckling period, the body length reaches 70-80 cm and weight 15-17 kg (Scheffer, 1950). The pups can withstand well all types of mechanical force and do not suffer serious damage even when pressed by a bull weighing 200 kg.

Pups are capable of staying in water a few days after birth but avoid the sea for 3-4 weeks. Only then do they begin to learn to swim in shallow water in calm weather. In August the pups go out to sea on their own and swim for long periods within sight of the coast. In September they are as adept as their parents at sea, at times venturing far out; by October-November they leave the islands for a pelagic mode of life.

On taking to independent feeding, the growth of young seals somewhat slows down initially but later proceeds steadily for up to 10-12 years. At this age the animals have reached full development and further growth wholly, or almost wholly ceases. Throughout the growth period males grow faster than females, as a result of which the adults of the two sexes differ considerably in size (Tables 9, 10, 11).

103 A large bull can weigh 285 kg and a large female 63 kg (Dorofeev, 1964).

102 Table 10. Change in body length (cm) of the fur seal with age (Arsen'ev and Fedorov, 1964)

Age, years	Males*		Females	
	Number in sample	Average length	Number in sample	Average length
1	28	78.5	14	76.0
2	30	96.5	4	95.3
3	52	107.5	3	100.7
4	12	121.7	36	109.3
5	9	129.1	55	115.5
6	9	142.5	45	121.3
7	7	148.2	66	121.4
8	5	162.9	105	123.6
9	8	168.7	143	125.3
10	5	175.9	129	124.3
11			137	127.9
12			106	126.6
13			120	126.5
14			108	128.4
15			67	129.9
16			51	130.4
17			46	127.6
18			23	129.1
19			19	130.7
20			6	130.0

*Adult bulls measure up to 200 cm or more.

103 Table 11. Change in weight (kg) of the fur seal with age (Arsen'ev and Fedorov, 1964)

Age, years	Males		Females	
	Number in sample	Average weight	Number in sample	Average weight
1	1	23.0	—	—
2	47	24.0	1	25.0
3	404	31.5	11	25.6
4	190	40.9	40	29.1
5	21	56.4	26	30.7
6	9	71.0	10	35.5
7	3	116.0	5	33.0
8	5	162.6	1	41.0
9	—	—	1	31.0
10+	—	—	8	38.5

The age of the fur seal is determined from the annual rings at the base of the upper canines (Scheffer, 1950). The number of layers in males corresponds to the number of years and, in females the first layer from

the tooth crown zone is ignored when counting the number of rings. The accuracy of determining the age based on these layers was verified in tagged seals (Fig. 74).

Some females attain sexual maturity and are impregnated for the first time in the third year but most mate in the fourth year, while the vast majority begin reproducing by the fifth year (Arsen'ev and Fedorov, 1964; Craig, 1964). Some whelp only in the 7th, 9th, and even the 12th year. The period of maximum fertility extends up to the age of 20 years although by this time there is a relative increase in sterility. It has been assumed that females retain their ability to reproduce throughout their life (Boitsov, 1934).

Spermatozoa have been reported sometimes in the testes of three-year-olds (Grebanskii, 1902; Boitsov, 1934); usually, however, males attain sexual maturity at 5-6 years of age and begin to mate even later. Seven-year-old bulls, because of their physical immaturity, still cannot occupy a place in the harem rookeries and are chased away by the more powerful older bulls. Even in the 8th year the bull is not always successful in forming his own harem (Fig. 75); if successful, he does not remain for long in the harem rookery. Apparently, the bull attains maximum strength by the age of 10 years (Fig. 75). The period of cessation of sexual activity in bulls has not been established. There is no information on longevity.

At 3-4 years of age the guard hairs on the nape of males begin to grow and form a "mane" which represents a secondary sex character. Even at 5 years of age the mane is quite visible and becomes very distinct in the subsequent year. This feature is fully developed with the onset of sexual maturity.

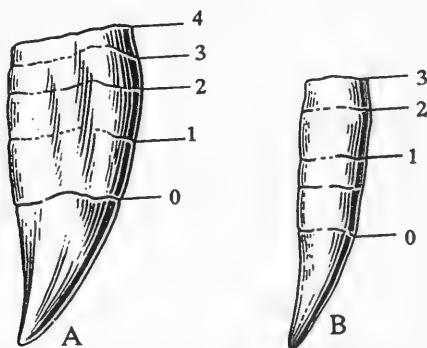


Fig. 74. Annual marks (layers) on the canines of fur seals. A—male, B—female (figure by N.N. Kondakov).



104 Fig. 75. Large bull fur seal with a harem. Bering Island, July, 1972 (photograph by S.A. Olekhnovskii).

Uterine molting has been noticed in embryos. During this period the primary pelage is replaced by infantile hair, which is seen in the newborns (Belkin, 1963). The hair coat of pups consists of soft black guard hair ("black" pups) and very low, rather poorly visible underfur. The first molt takes place roughly a month after birth. As molting progresses, the black guard hairs are shed and brownish underfur grows vigorously; as a result the pups change from lustrous black to dull brown. Later, the guard hairs are shed and replaced by new hairs that are gray, changing again the overall color of the pup. By four months of age, the pup completes the first molt and acquires a beautiful silver-gray coat. The end of molt coincides with the pups leaving the island and taking to a pelagic mode of life.

Molting of young males (bachelors) occurs partially during their residence in coastal rookeries; some even arrive on the island in the initial stage of molt. The very young males (one or two years old) are the first to molt, followed by the older ones. Molting peaks in September-October; however, not all animals molt on the coast and the process is completed at sea.

Molting of maturing and young bulls on Tyulen' Island was observed at the end of September. Three observations have been reported of traces of nitrolacquer (used for marking in the preceding year) on the hair coat of old bulls. It is possible that some old bulls do not molt every year. It is

thought that moderate molting continues until January and February of the following year (Scheffer, 1962; Scheffer and Jonson, 1963; Bychkov, 1964).

Molting of females commences in August after whelping, and coincides with the period of suckling. Evidently, molting is not yet complete when the females leave the coast by November and is completed at sea.

Molting of the hair coat commences on the head, at the base of the fore flippers, and at the tail end of the trunk. Molting then gradually extends to the sides, back, and belly. During molt new hairs fully replace the old. Even the fur hairs molt. Whiskers do not molt but, with the onset of sexual maturity, they become gradually depigmented.

105 *Enemies, diseases, parasites, mortality, and competitors.* The fur seals have no enemies in the coastal rookeries. At sea they are sometimes attacked by the killer whale (*Orcinus orca*).

Newborn pups are known to suffer from uncinariasis caused by intestinal parasites, most often causing the death of the pup. Instances are known of inflammation of the respiratory tract and intestine. Adults suffer from diseases of the eyes, sometimes resulting in blindness. Skin diseases resembling scabies have been reported (Boitsov, 1934). On the Commander Islands, bronchial, gastric, and intestinal catarrh, infectious paratyphoid, and dermal herpes have been reported. On Tyulen' Island, there have been instances of bilateral pyelonephritis, hemorrhagic meningitis, peritonitis, and endocarditis (Dorofeev, 1964). In the blood of 18 fur seals (34 examined) on the Commander Islands, microfilariae of an indeterminate species, were detected (Delyamure *et al.*, 1961).

Two species of lice parasitize the skin of the fur seal: *Antarctophthirus callorhini* (Osborn, 1899, McAtee) and *Proechinophthirus fluctus* Ferris, 1916, Ewing. Parasitic mites have been detected in the nasopharynx (*Orthohalarachne attenuata* Newell) and in the trachea and bronchi (*Orthohalarachne diminuata* Newell).

Nineteen species of helminths have been recorded: one species of trematode and six species each of cestodes, nematodes, and acanthocephalans. The trematode, *Phocitrema fusiforme* Goto and Ozaki, localizes in the intestine (known also in ringed seals and sea otters). Of the cestodes, *Adenocephalus septentrionalis* Nybelin parasitizes the large intestine (not known in other animals) and *Clestobothrium glaciale* Cholodkovsky is found in the intestines. *Diphyllbothrium krotovi* Delamure has been detected in the small intestine of only fur seals. *Diphyllbothrium* (*Bothriocephalus*) *lanceolatum* Krabbe, quite a common parasite of marine mammals, is found in the intestine of fur seals and *Diphyllbothrium tetrapterus* Sibold, in addition to the fur seal, is found in

some other species of pinnipeds. Finally, *Diphyllbothrium macrocephalus* Linstow, in addition to fur seals, has been reported only in bearded seals. The nematode, *Contracaecum osculatum osculatum* Rudolphi, found in fur seals, parasitizes the small intestine and stomach of many marine mammals in both hemispheres; *Phocascaris phocae* Höst, also known in the Greenland seal, has been detected in the duodenum and in the small intestine. *Terranova decipiens* Krabbe parasitizes the fur seal and many species of pinnipeds of both hemispheres, and is also recorded from some cetaceans. *Terranova azarasi* Yamaguti and Arima is known only in pinnipeds. *Anisakis pacificus* A. Skrjabin, known also in the three species of cetaceans, has been found in the intestine. In the small intestine of fur seals, especially in yearlings, the nematode *Uncinaria lucasi* Stiles has been detected. From the acanthocephalans, *Corynosoma strumosum* Rudolphi has been reported in almost all the pinnipeds of the Northern and Southern hemispheres, in two species of cetaceans, in land mammals (cats and dogs), and in many species of birds. *Corynosoma ventronudum* A. Skrjabin has been found in the intestines of only Steller's sea lions and the northern fur seals. Of the two species of intestinal parasites, *Corynosoma semerme* Forsell is reported from many other marine animals and birds, while *Corynosoma villosum* van Cleave only from fur seals. *Bolbosoma bobrovoi* Krotov and Delamure, found in the small intestine of northern fur seals, is also found in Steller's sea lions and *Bolbosoma nipponicum* Yamaguti, parasitizing the small intestine and cecum, has been found in three species of whales and ringed seals. The helminths found in various populations of the northern fur seal are listed in Table 12.

The largest number of species (13) of helminths is known in the Commander fur seals and only two species are common for all the three subspecies. In the southern fur seal, seven species of helminths are found, of which only one (*Terranova decipiens*) is known only in the northern fur seal (Margolis, 1954; Delyamure, 1955; Olsen, 1958; A. Skryabin, 1958; Delyamure and A. Skryabin, 1960).

Mortality is maximum in infancy, mainly in the first one-and-a-half months after birth. With the disbanding of harems (from early August), the mortality of pups declines considerably. Mortality varies widely in different years but usually does not exceed 16-17% of those born. The main cause of pup mortality on the Pribilof Islands is the intestinal parasite *Uncinaria lucasi*, which causes anemia and emaciation. Other causes are trauma inflicted by adult fur seals or injuries caused by falling from cliffs where the pups gather quite eagerly. A relatively large number of pups perish from starvation when they lose their mothers. Instances of mortality caused by bronchial inflammation of the lungs are also known.

106 Table 12. Helminths in the northern fur seal (Delyamure and A. Skryabin, 1960)

Helminth species	Subspecies of fur seals		
	Commander	Kuril	Alaskan
<i>Phocitrema fusiforme</i>	+		
<i>Adenocephalus septentrionalis</i>	+		
<i>Cestobothrium glaciale</i>	+		
<i>Diphyllbothrium krotovi</i>	+	+	+
<i>Diphyllbothrium lanceolatum</i>	+		
<i>Diphyllbothrium macrocephalus</i>	+		
<i>Diphyllbothrium tetrapterus</i>			+
<i>Anisakis pacificus</i>	+		
<i>Contracaecum osculatum</i>	+		
<i>Phocascaris phocae</i>	+	+	
<i>Terranova azarasi</i>	+		
<i>Terranova decipiens</i>	+	+	+
<i>Uncinaria lucasi</i>			+
<i>Bolbosoma bobrovoi</i>		+	
<i>Bolbosoma nipponicum</i>		+	
<i>Corynosoma semerme</i>			+
<i>Corynosoma villosum</i>			+
<i>Corynosoma strumosum</i>	+		+
<i>Corynosoma ventronudum</i>	+		

*At the end of the 1960s *U. lucasi* was also recorded from the seals of Bering Island (V.A.).

The extent of mortality increases in years of unfavorable climatic conditions. In 1965, on Tyulen' Island, a catastrophic mortality of pups resulted from severe and prolonged storms; waves flooded the harems and washed away pups which had yet to gather strength. Over 20,000 pups perished (some 40% of those born that year). However, such cases are extremely rare. Mortality also increases with increasing population, i.e., crowding in the rookery.

The mortality rate in the rest of the age groups in the coastal rookeries is very small, only a few tens [of seals]. Adults die mainly at sea. Young ones, especially those born in that year and the yearlings incapable of withstanding severe storm conditions, experience difficulties in getting at food and die of starvation. The mortality of the Pribilof females was mathematically computed as 18% for eight-year-olds, 20% for nine-year-olds, 19% for ten-year-olds, and 25% for 12-year-olds and beyond (average 20%) (Nagasaki, 1961; Chapman, 1961). Considering these values as high, American scientists use, in different calculations, three mean mortality coefficients for females of all ages: 5%, 10%, and 15%. This question has not been finally resolved.

At different times of the year, different types of competition arise between the northern fur seals and Steller's sea lions, these being most pronounced in the period of life in the coastal rookeries. These competitions are mostly determined by the numerical ratios of these two species. A relatively simple form of competition has been observed on 107 Mednyi Island (Commander Islands) where in summer some 100,000 fur seals and 4,000-5,000 Steller's sea lions live side by side (Fig. 76). The fur seals form dense harems while the sea lions are represented mainly by young immature males. At the end of the 1960s, the number of old male sea lions began to increase, mature females appeared, and sometimes even small harems were formed. The interrelations of these two species of animals vary slightly with the varying herd structure of the sea lions. The reproducing sea lions (especially the bulls) are the most aggressive toward the fur seals (S.V. Marakov). The fur seals spend only the summer on the island while the sea lions live there throughout the year, their numbers increasing significantly in winter.



107 Fig. 76. Steller's sea lion, *Eumetopias jubatus*, in a rookery of the northern fur seal. Mednyi Island (photograph by S.V. Marakov).

In early spring Steller's sea lions occupy much of the territory of the northern fur seals and the fur seal bulls are compelled to put up with the stronger and more powerful Steller's sea lions. However, as the fur seal females start arriving, the sea lions gradually vacate the rookeries for the bachelor quarters and isolated boulders scattered abundantly on the island coasts. It cannot be said that the sea lions are forced out by the growing harems of the fur seals because they invariably leave the rookery in the wake of the en masse invasion of female fur seals. When hunting for fur seals commences, the Steller's sea lions leave even the bachelor quarters. However, some sea lions do remain and are even caught along with the fur seals. As the harem activity abates, harems disband, and hunting for the fur seals ceases, the sea lions again partially occupy the harem rookeries in which the two species coexist peacefully (Muzhchinkin, 1964). A similar picture, but involving a smaller number of Steller's sea lions, is observed on Bering Island.

Such interrelations are suggestive more of coexistence than of competition, but there is a view that sea lions inflict damage on fur seals and are, therefore, undesirable inhabitants of the rookeries (Marakov and Nesterov, 1958).

108 Sometimes fur seals of unusual color—rust, light cinnamon, etc., have been found. In a rookery on the Commander Islands, a bright rusty female was seen suckling a normally colored pup; at another place a large well-fed pup of chocolate color was seen. On Tyulen' Island a bull of normal size but of yellow color was found in a harem. However, colored fur seals are usually seen among small-sized animals, females and young males (V.A. Arsen'ev). According to hunters (S.P. Naumov, 1933), male sea lions ravish the female fur seals, but the fur of the offspring is poor and is rejected in trade. There is no precise proof for this statement and it is probably erroneous as successful crossing of such taxonomically distant animals is impossible. Without ruling out attempts at crossing Steller's sea lion with fur seals, it may be said that fur seals exhibiting aberrations from typical coloration are considered hybrids.

Another form of relationship has been noticed on some islands of the Kuril range in which separate harems of both species are formed in the same rookeries and their offspring born. But such rookeries are small and the population of animals is much less than on the Commander Islands. During June such rookeries are occupied by harems of the sea lion, among which whelping is at its peak. The fur seal bulls arriving in early June and the females in the latter half of this month, are forced to huddle together along the fringes or occupy the free sections for raising their pups. In this period, the large and powerful sea lions totally dominate the fur seals.



108 Fig. 77. Female northern fur seal. Bering Island, November, 1965 (photograph
by S.V. Marakov).

In early July the harem life of Steller's sea lions becomes calmer, their numbers on the beach diminish rapidly, and pups begin to enter the sea freely; most of the sea lions migrate to other sites or even to an adjoining island. The small number of sea lions remaining in the rookery no longer disturb the growing harems of the fur seals, whose harem life
109 is now beginning to reach its peak. But even at this time the sea lion bulls remaining in the rookery move freely throughout, chasing the fur seal females and bulls without heed for their belligerency. Such instances are not frequent, however. The differences in the whelping periods of fur seals and sea lions largely smoothen the competition between them and help the weaker fur seals to occupy the harem territories vacated by the sea lions and to spend a normal breeding season (Belkin, 1966a).

The fur seals and sea lions cohabiting in summer could quite often face competition for food, as many items are common to the two species. However, in most cases such competition is inconsequential. The fur seals of the Commander Islands feed mainly on pelagic animals while the sea lions feed on demersals (Barabash-Nikiforov, 1936). Fur seals and sea lions are seen swimming along the coasts of British Columbia. At this time the fur seals are dispersed farther from the coasts and feed

mostly on schools of small fish and squids at the water surface; meanwhile the sea lions remain closer to the coasts and feed on demersal fishes and octopuses, their primary food. In this region, however, there are about ten species of animals which serve as food for both fur seals and sea lions (Spalding, 1964a*).

Population dynamics. The dynamics of the natural populations of all the fur seals has not been studied. It is perhaps insignificant since instances of en masse mortality due to natural factors have not been reported. Very soon after the islands on which rookeries are located were opened to hunters, herds of fur seals and the populations of all the three subspecies suffered large variations time and again, as a result of human intervention.

The rapacious exploitation of the Tyulen' Island stock began immediately after the island was discovered in the mid-nineteenth century, and some 100,000 fur seals were caught there during 1852-1855. The stock was destroyed and only gradually replenished during the 14 years in which hunting was banned. In 1870, the population was again destroyed and unrestricted hunting prevented its restoration for a long time. The fur seal population was so small (not more than 7,000 in 1911) that for over 20 years (roughly 1895-1923) the annual catch did not exceed 500 fur seals. In 1911, the Convention for the Protection of the Northern Fur Seal was signed and, as a result of rational exploitation, the population was gradually reconstituted. This helped to raise the annual catch to 2,000-3,000 animals by 1942. At the end of World War II, before transferring the island to the USSR, the Japanese caught over 50,000 fur seals in four years, which again brought the stock to the brink of disaster. Besides hunting fur seals on the coast, their hunting at sea flourished and was most rapacious as more than one-half of the sea catch comprised females, most of them gestating.

In 1957, the USSR, the USA, Canada, and Japan signed a new Provisional Convention for the Protection of the Fur Seal in the northern part of the Pacific Ocean, the most important provision of which was a ban on hunting at sea (a limited catch was permitted by each country exclusively for research). This encouraged the development of a scientifically organized, rational fur seal industry on the islands where, according to the rules laid down, only the young males possessing the most valuable coats were permitted to be killed.

A census was undertaken to determine the populations. Two groups of northern fur seal bulls and newborn pups could be counted quite accurately. The former were easy to enumerate in a rookery. The pups were counted by chasing them with a chain past the counting device. Simultaneous with live pups, dead ones too were counted and their total

yielded the total number of mothers. By determining the number of parents of both sexes, the number of young males that could be killed
 110 was calculated in such a way that the required number of male parents for normal reproduction was ensured (Dorofeev, 1958, 1960).

The ban on killing females, fixing a rational number of bachelors that could be killed, and maintaining the natural regime of harem rookeries during the breeding season led to a comparatively rapid growth of the population of fur seals on Tyulen' Island. By 1960, the total population approached 100,000, and 6-7 years later to 160,000-170,000. Adoption of the principles of rational killing and the ban on hunting at sea, enabled a steady population growth. An obstacle to the growth of stock on Tyulen' Island is the limited free territory for enlarging the harems, due to the island's small size.

The fur seal rookeries on the Kuril Islands have always been small and thus there was no coastal hunting there; but rapacious hunting at sea led to the near total extermination of the rookeries. After the 1957 Convention, the fur seal stock was gradually restored to about 15,000 by 1966 (Uspenskii, 1955; Klumov, 1957; Belkin, 1965a*).

Immediately following the discovery of the Commander Islands by Vitus Bering in 1741, the fur seal stock there began to be exploited. According to the eyewitness accounts of early investigators, the fur seal population at that time was in the millions. By 1786, over 64,000 seals had been killed. Individuals as well as organized companies hunted at different periods. Each "owner," before transferring his rights to the next, tried to extract the maximum benefit. Moreover, for many years gray seals, i.e., pups were also killed. The killing of infants depleted the herds so much that hunting had to be almost prohibited. From 1843 through 1847, a complete ban was imposed, but this did little to restore the stock. Later, restricted and rapacious hunting alternated; killing of the young was banned in 1871 and judicious hunting of bachelors initiated. The herds gradually began to replenish themselves. But by then hunting at sea had begun anew and from 1891, in which year an agreement was signed between the USA and the UK for immediate cessation of hunting in the eastern part of the Pacific Ocean, there was extreme irrational killing of the Commander and Tyulen' populations by the Japanese. As a result of the combined effect of all these factors, by 1911 the Commander population had dwindled to a mere 9,000.

After several negotiations between Russia, the USA, the UK (also representing Canada), and Japan, the Convention for the Preservation of Fur Seals was concluded for the first time in 1911 and remained in effect until 1940. During World War II, Japan unilaterally breached this Convention. Although the Convention formally banned sealing at sea, there

was regular rapacious killing in the western part of the Pacific Ocean during the six months in which the fur seals remained at sea under the protection of no one. Further, the system of organized coastal hunting was far from perfected. All these factors contributed to the extremely slow restoration of the Commander fur seal stock.

After concluding the Provisional Convention of 1957, a gradual restoration of the stock was achieved by organized hunting. By 1960, the population of the Commander fur seal had increased to nearly 100,000 and later reached almost 200,000.

On the Commander Islands there are numerous deserted rookeries and much free territory suitable for the formation of new rookeries. Therefore, cessation of hunting, or properly organized hunting, could encourage an increase in the number of rookeries and, perhaps, gradually restore the fur seal population to its original glory.

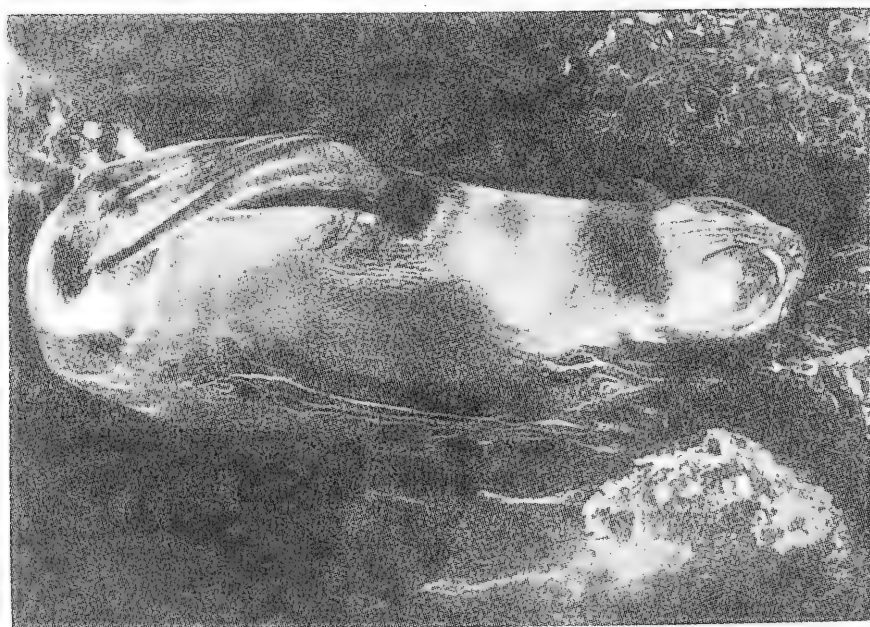
The Pribilof Islands were discovered in 1786 but, unlike on the Commander Islands, until 1799 seal hunting was done only by Aleutian emigrants. Later, as on the Commander Islands, an avaricious killing of seal herds began, sharply reducing the animal population. In 1867, Alaska (and the Pribilof Islands) came under the USA and from 1870 the US government restricted seal hunting, leasing only under the condition that killing would be restricted to the islands and that females could not be killed. Later, the hunting season and the annual quota were fixed. From 1910, the leasing system was abolished and the government established its control over fur seal hunting. As a result of the measures adopted,



Fig. 78. Young female sleeping on the coast. Bering Island, July, 1967 (photograph by P.G. Nikulin).

the Pribilov stock was far better maintained than the Commander and Tyulen' stocks, and by 1911 comprised some 200,000 animals. From the moment the 1911 Convention was signed, Americans constantly protected their stock over the migration route and also in the region of wintering, using armed ships, thereby totally abolishing the carnage at sea and establishing a quite rapid growth rate of the stock. The population of the Pribilov fur seal had crossed the 1.5 million mark by the 1950s.

American scientists believed that the population had exceeded the optimal level by that time, not only preventing further increase of stock, but also leading to high mortality of the offspring and even to some loss of adults. As a corrective measure, hunting of females was permitted on the Pribiloy Islands, which in some years exceeded 40,000. Theoretically, for a normal state of population, the annual addition of pups should not exceed 500,000-550,000. This objective was achieved by 1966. In order to maintain the stock at a stable level (about 2 million), hunting quotas were proposed at approximately 60,000 males and 10,000-12,000 females per year (Nagasaki, 1961; Chapman, 1961; Baker *et al.*, 1963; Dorofeev, 1964; Roppel and Davey,* 1965).



The population dynamics of the northern fur seal could serve as a striking example of the adverse influence of the activity of man on a flourishing population, and of the possibility of restoring it by rational utilization of the animal.¹⁵

Field characteristics. Adult males are large and females of moderate size. The newborns are black in color, turning gray by the time suckling ceases. The fur of the older animals is in various shades of cinnamon-brown. The hair coat of bulls is a dark brown or gray, more often monochromatic. Hairs on the nape of bulls are long and form a "mane". The pinnae are narrow and pointed. The fore and hind flippers are long and their outer tips without fur; the hind flippers fold under the trunk.

In summer the animals gather into large herds on the coasts and form harems. The northern fur seal makes various sounds. Bulls groan in a deep-drawn bass and during brawls make frequent guttural sounds; the voice of females and the young sounds from afar like the bleating of sheep, and that of newborns like the bleating of lambs. In water the animals remain singly or in small groups; while resting on their back, they raise the long hind flippers which, from a distance, resemble a sail.

The northern fur seal is readily distinguished from a sea lion, quite similar to it, by much darker coloration, smaller size, and the absence of an upturned nose. (V.A.)

Economic Importance

Concurrent with the increment in stock, which commenced after the 1957 Convention, there has been a gradual increase in number of fur seals caught. By 1967, the total catch of the USSR had reached 20,000.

Because the fur coat is highly prized, seal hunting is of considerable economic importance. Depending on world market conditions, the furs are valued on average at US \$100 apiece, with some fetching as much as \$160. Apart from the fur, fur seals provide a comparatively large quantity
113 of byproducts—meat, blubber, and liver. The carcass is used for feeding ranch-maintained fur animals, while the oil melted from the blubber has a commercial value. The liver is a source of vitamin A.

The technique for catching fur seals is extremely primitive but has not changed over the years. The animal is stunned by a blow on the head

¹⁵ During 1963-1965 there was a marked decline in all the populations of fur seals, which sharply reduced the number of bulls, the annual increment in pups born, and the population of bachelors. This reduced the overall population. The reasons for the decline have not been ascertained (V.A.).

with a club, preferably in the nasal region. More modern methods using electricity, soporifics, and immobilizing agents are being developed.

Bachelors aged 3-5 years, settled on the fringes of harems or at some distance from them, are the targets of hunters. In the predawn hours the hunting party first surrounds the bachelor quarters, thus barring their access to the sea. The cordoned-off herd (sometimes up to 1,000 strong) is slowly chased aside to the slaughter zone, giving the animals frequent rests of 5-10 min. If rapidly chased, the fur seal warms up and can die of heat shock (sunburn). In such animals the hair falls out and the skin has to be rejected. On arrival at the slaughter zone, the large herd is separated into small groups of 15-20 animals and graded. Bulls, females, and small-sized animals are freed in the sea and the rest clubbed to death as described above. After the blow, the seal is slit open with a dagger-type knife in the heart region. As soon as bleeding commences, the dead animal is skinned together with the blubber; the skin at this stage is called a raw hide. Later, the blubber is removed using a blunt knife. The skins, free of flesh are washed in cold water (sea water) and salted, using common salt. The preserved skins are packed in drums and dispatched to the fur factory for making semifinished products.

Seal hunting has acquired proper organization. The hunting period (June 1 through August 1) has been fixed and the annual quota of kills determined to ensure the future growth of the stock; killing of females has been banned. Offspring and parents are regularly counted. If the number of bulls exceeds the required number (in a restricted rookery), the excess number is killed. The commercial catch of bachelors is limited to 16 to 20% of the population of each generation. All of these measures promote the growth of the stock and help increase the catch year after year without decimating the population. In this way it is wholly possible to steadily increase the seal population. However, the decline in population has greatly reduced the number of animals killed annually to 6,000-8,000 in the USSR, and from 50,000-60,000 to 32,000-35,000 in the USA. Given such a situation, a partial or even total ban on seal hunting appears necessary for restoration of the population strength. (V.A.)

SUPERFAMILY OF EARLESS, OR TRUE, SEALS

Superfamily PHOCOIDEA Smirnov, 1908

Family of True Seals

Family PHOCIDAE Gray, 1825

These pinnipeds are extremely diverse in size, ranging from the smallest to the largest in the order, and are least adapted to movement on

114 hard substrates because of their inability to raise the trunk on the hind limbs (which are turned backward and incapable of bending forward at the calcaneal joint) and also because of their shortened and weak fore flippers. The fore flippers have well-developed long claws which are not strongly uncinatate or sharply compressed from the sides. The hind flippers too have claws, though considerably reduced in some species, especially among 8-incisored seals. The fore as well as the hind flippers are covered with hair. The digits of the fore flippers, though enclosed in a common skin, fold up to the last phalanx and possess relatively high mobility at the joints, which enables the animal to clutch projections on the ground and dig in, and to use them to puncture very dense snow or even to scrape ice. However, the reach of the hand is extremely restricted, unlike the hind flippers in which, on the contrary, the rays are covered in a better developed and elastic skin membrane and are capable of considerable movement by forming a broad fan-shaped oar.

Ear pinnae are altogether absent. The ear openings are densely covered and appear as small patches of exposed skin.

The head is usually rounded, shortened; the snout is not pointed but only slightly compressed dorsoventrally and is covered with many labial whiskers arranged generally in 5-7 arcuate rows oriented along the line of the mouth. Their total number on each side of the mouth is about 50-60. With rare exceptions, the whiskers are flattened and have wavy edges (Fig. 81). Whiskers are also present above the eyes (not more than seven above each) and on the upper side of the rostrum close to the nostrils (one or two on each side). The cutaneous glands are not developed to the same extent in the different species; the sebaceous glands generally function well, while the sweat glands are often poorly developed and are not seen at all in some individuals. A scrotum is absent. The tail is sufficiently well developed and flattened dorsoventrally.

In general build the species of the family are rather similar, varying mainly in size and weight, shape of the head, snout projection, structure of the fore flippers, depth of incision of the hind flippers, growth of the claws, and number of whiskers.

The skull has a spacious cranium with a very narrow interorbital space and widely separated zygomatic arches; the crests [sagittal, temporal] on the flattened upper side of the cranial portion are not developed and the top profile is usually less curved. The bony tympanic bullae (bullae osseae) are large and bulging, with a fairly smooth, hemispherical, sometimes slightly flattened surface of different profiles and a well-developed bony [external] auditory meatus, which in most (subfamily of true or 10-incisored seals, *Phocinae*) has a well-developed bony cavity on its outer side. The mastoid process is relatively small, not fused

with the paroccipital and not directed downward. An alisphenoid canal is absent. Nasal bones terminate posteriorly in a common wedge-shaped apex protruding into the anterior portion of the frontal bones (Fig. 7). The zygomatic bones lack a distinct anterior lower process (Fig. 8).

The molars and most of the premolars (except the first) have two roots in the vast majority of the species. Teeth crowns are quite compressed laterally and in most cases are complex with additional cusps at the back and in front of the main cusp. The dental formula varies mainly in the number of incisors from 3/2 to 2/1. The complete dental formula for the main group of the family (10-incisored seals) is:

$$I \frac{3}{2}, C \frac{1}{1}, P \frac{4}{4}, M \frac{1}{1} = 34.$$

Canines are usually not well developed, but are longer and more massive predominantly in the large and more predaceous species (elephant seal, hooded seal, leopard seal, monk seal, and larga.

- 115 The cecum is poorly developed, usually not longer than 3 cm. The glans penis is smooth, without spines. The os penis is faintly curved, quite thickened near the proximal end, and without transverse forked or T-shaped tip distally.

The majority of the species have one pair of teats, very rarely two.

The hair coat after shedding of the juvenile (or embryonic) fur is short, tough, with weakly developed fur hairs that do not form a distinct layer of underfur. The hair tufts have only one to five fur hairs 5 to 9 mm long; the guard hairs are 12 to 18 mm long. The juvenile (embryonic) coat [Lanugo] with which the pups of many pagophilic species are born is, on the other hand, extremely luxuriant, dense, and thick, affording good protection from wind and frost in the severe arctic and subarctic climate. The juvenile hairs, mainly white, with cream, green, or gray tones, are sported for not more than four weeks (often for a much shorter duration); sometimes they are shed in the fetal membranes even before birth (hooded, bearded, and common seals). After the first molt, the color of the hair coat changes sharply but it takes several years for the definitive features of the species to develop. Adults sport a spotted, sometimes even sharply contrasting coloration (Greenland [harp] and ribbon seals). Nevertheless, seals with a wholly monochromatic coloration are not rare (Baikal seal).

Sexual dimorphism is manifest among many species, mainly in coloration, body and skull dimensions, and other features. In some species

(elephant seal, hooded seal) this dimorphism is very sharply manifest in body size, weight and structure of the snout.

The size difference between seals of various species is highly significant. The largest member of the family (although not typical of our fauna), i.e., the elephant seal of the Southern hemisphere (*Mirounga leonina*), measures (male) 6 m or more (up to 6.5 m) in length along the dorsal surface (L_c) and weighs up to 4-5 tons. On the other hand, most of the small-sized races of the ringed seal and Caspian seal attain sexual maturity at 120-140 cm length (L_c); their weight at the lowest feeding level (late spring) drops to 35-40 kg. In the Okhotsk ringed seal (akiba) the weight drops, on average, to 24.5 kg (females) and 26.0 kg (males) (Fedoseev, 1971). In spite of such large differences in dimensions and weight, the length ratio between the extremes is relatively small (see p. 8) at roughly 1:5, but the weight ratio is quite significant at 1:200.

In spite of the great similarities in general appearance, the species of the family differ significantly in mode of life, site selection for breeding and molt, and also in food specialization. Only one species, the leopard seal (*Hydrurga leptonyx*), relies on warm-blooded animals for food and feeds not only on penguins and seals, but also on large fish (see p. 11). On the other hand, there are species feeding almost exclusively or mainly on invertebrates—planktonic crustaceans (crabeater seal, *Lobodon carcinophaga*) or various species of benthos, mainly mollusks and crustaceans (bearded seal). Many other species of seals live mainly on fish, some on larger (hooded seal, gray seal, and others), others on smaller ones (ringed, Caspian, and Baikal seals). Some seals also consume cephalopod mollusks (hooded, gray, Greenland, ribbon, and others) or small crustaceans (ringed seal, sometimes larga, Greenland seal, and others). The depth of submergence of these seals also varies. The deepest divers are the hooded seal (perhaps the elephant seal also), Weddell's seal (*Leptonychotes weddelli*), which dives to a depth of 400-600 m, and the ribbon seal, and probably even the gray seal.

No sharp differences in the daily behavior and activity of these animals have been recorded; they move around and feed at any time.

- 116 Most species perform significant migrations under the influence of various factors—seasonal movements of the main food organisms, changes of temperature conditions consequent to changes in ice conditions, and also the need for specific conditions for reproduction. Migration invariably conforms to an exact pattern—easily distinguished from local movements—with some animals straying far from their usual habitats (e.g., ringed seal in the circumpolar regions; hooded seal in the

White Sea or in the eastern Atlantic far south of the polar circle, and large on the shores of China).

True polygamy is rare among the members of this family (most distinct among the elephant seal, *Mirounga leonina*). On the other hand, strict monogamy is likewise not very characteristic of true seals since the males and females meet for a very brief mating season.

Males do not share the responsibility of raising the pups (as in the other families). Pups are usually delivered one in a season (twins are extremely rare). Apparently the pups are capable of displaying complex forms of higher nervous activity.

The members of the family are distributed in all the seas north of the subtropics: in the Atlantic and Pacific oceans and everywhere in the Arctic Ocean, in some landlocked water bodies (Black, Caspian, and Baltic seas and lakes Baikal, Ladoga, and others) and also in a fairly broad ocean belt surrounding Antarctica, with some ranges (mainly those of the elephant seal) projecting northward as "tongues" at places (along the American, African, and Australian coasts).

The range of the family in the Pacific Ocean region encircles the western, northern, and eastern fringes of the sea in the form of a narrow arc. Its boundary passes from northern China and the Korean Peninsula along the western part of the Sea of Japan, covers the coastal regions of the northern half of Japan and extends along the eastern flanks of the Kuril range including the Sea of Okhotsk, continues along the eastern coast of Kamchatka to the Commander Islands, from where it bends sharply to the east along the Aleutian Islands and reaches the coastal belt of the American continent, from where it descends south to southern California (Fig. 80).

The range of the family in the North Atlantic wholly coincides with the range of the order (since the members of the family of eared seals are absent there and the range of the walrus does not extend beyond the range of the family). The range of the family of true seals in the Southern hemisphere coincides generally with that of the order but does not extend as far northward along the South American coasts, stops short of reaching South Africa and only partly covers the coastal waters of southern Australia (mainly Tasmania). In the Arctic Ocean the range of the family coincides wholly with that of the order.

The range of the monk seal underwent the most significant variations over the historic past while the Caribbean monk seal is totally extinct (p. 500) and the range of the Pacific Ocean species is restricted to a negligibly small relict section of the Hawaiian Islands. In fact, even the European range of the monk seal, which is facing total extinction, is presently fragmented.

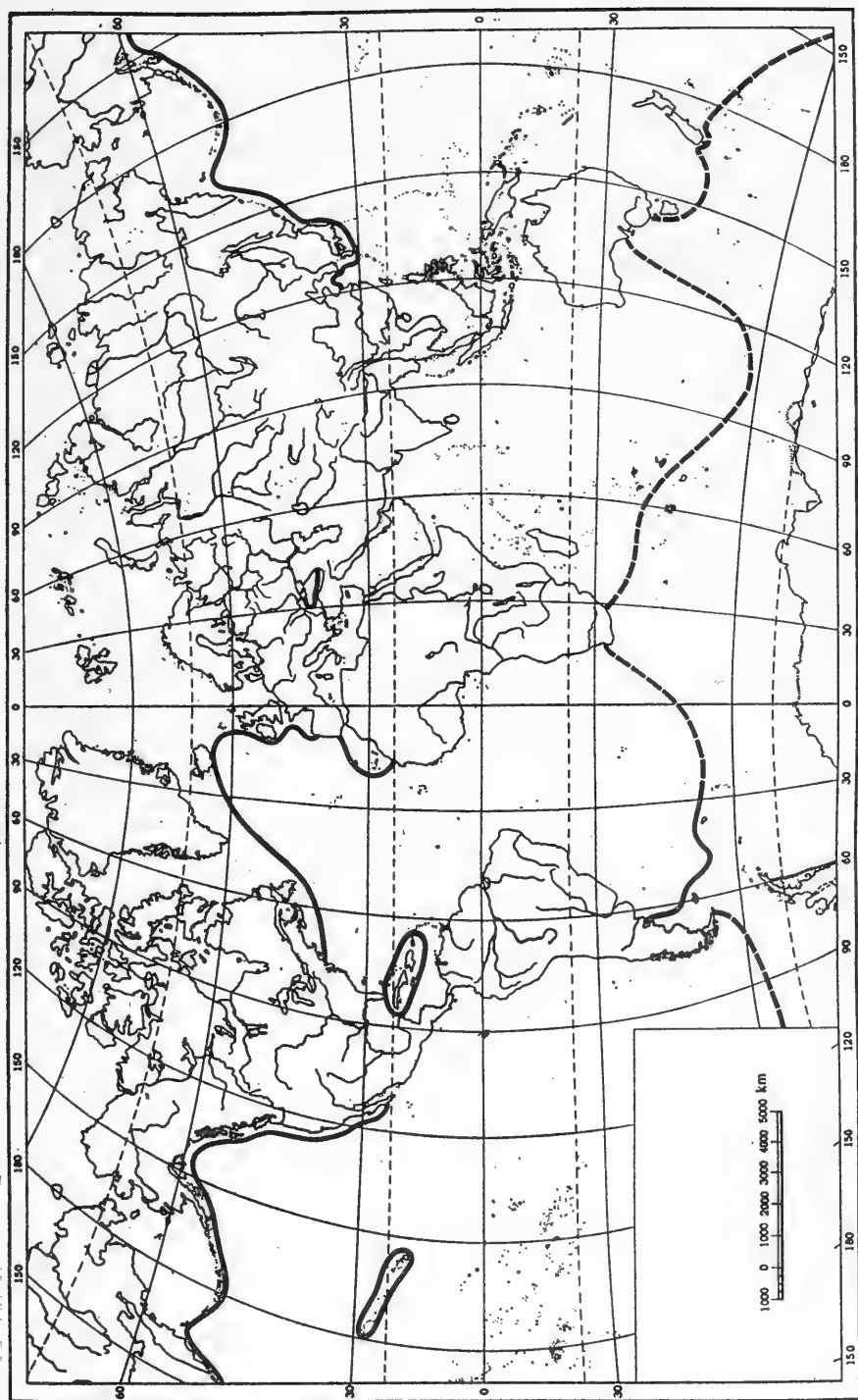


Fig. 80. Reconstructed range of the family of true seals, Phocidae. The southern boundary of the range (except the Black Sea) is shown in the Northern hemisphere and the northern boundary in the Southern hemisphere. Broken line depicts the probable boundary of the range (K.K. Chapskii).

The taxonomic features of the family are so sharp and cover so organically all the members of the family, at the same time distinguishing them from all other Pinnipedia, that the isolation and status of the family cannot be disputed. Although there is a tendency to question the entirety and rank of the order of Pinnipedia based on serological data (see under characteristics of the order), the unity of the family as such is beyond doubt. If, however, the diphyletic origin of the Pinnipedia is supported, 118 then the family of mustelids (Mustelidae) is evidently closest to the family of true seals from the canoid (arctoid) carnivores.

The earless seals, Phocidae, originated almost as long ago as the eared seals, Otariidae. Although the finds of the latter pertain to a somewhat earlier period (Lower Miocene) compared to the true seals (Middle Miocene), they are not so far apart to assume the origin of one group from the other. The Lower Miocene Pinnipedia already possessed the distinct features of the eared seals, Otariidae, and hence could hardly have been the base stock for the Phocidae.

The prevailing division of the family into subfamilies is extremely simple and has been generally accepted to date. The number of incisors forms the basis of the division. Three subfamilies are usually recognized: 1) Phocinae, 10-incisored ($I \frac{3}{2}$) seals covering the genera of ringed seals and true seals *Phoca* (including *Pusa*, *Pagophoca*, *Pagophilus*, or *Histiophoca*), gray seals (*Halichoerus*), and bearded seals (*Erignathus*); 2) Monachinae, 8-incisored ($I \frac{2}{2}$) seals of the subtropical regions of the Northern hemisphere covering monk seals (*Monachus*) as also the antarctic seals *Lobodon*, *Ommatophoca*, *Hydrurga*, and *Leptonychotes*; and 3) Cystophorinae, 6-incisored ($I \frac{1}{2}$) seals covering the genera of hooded seals (*Cystophora*) and elephant seals (*Mirounga*).

Some scientists (Gill, 1866; Gray, 1869; Kellogg, 1922; Simpson, 1945; and others) isolate Lobodoninae (Stenorhynchinae) into a distinct subfamily. These are the antarctic 8-incisored seals (Weddell's seal, *Leptonychotes*; Ross' seal, *Ommatophoca*; crabeater seal, *Lobodon*; and leopard seal, *Hydrurga*). There was, until recently, a tendency to place the elephant seal, *Mirounga*, in this group (King, 1966), which is hardly justifiable. There was also a suggestion to eliminate altogether the subfamily Cystophorinae. In spite of the osteological features which bring the genus *Cystophora* (hooded seals) close to the 10-incisored seals (spacious for. lacerum posterius, presence of for. entepicondyloideum, and so forth) and separating it from the genus *Mirounga* (elephant seals) bearing some features characteristic of the antarctic 8-incisored seals (highly reduced for. lacerum posterius in the skull, the same foramen in the humerus, etc.), there are many features (including some in the

basal and contiguous zones of the skull) which provide a no less weighty justification in favor of maintaining the prevailing division of the family.

Various authors assign a different number of genera to the family. There is a tendency to enlarge the number of Recent genera to 11 (Smirnov, 1929, 1935), 12 (Ognev, 1935; Chapskii, 1955), and up to 13 (Scheffer, 1958; Chapskii, 1963; King, 1966). The present publication has adopted the principle of a more extensive interpretation of the concept of the genus and thus 10 Recent genera are included in the family. Hence, together with the fossils, the family consists of a total of 22 genera. Of these, 10 belong to Phocinae, of which three are extant genera (*Phoca*, *Halichoerus*, and *Erignathus*) and seven fossil (*Prophoca*, *Callophoca*, *Gryphoca*, *Platyphoca*, *Phocanella*, *Leptophoca*, and *Miophoca*); nine to Monachinae (including Lobodoninae), of which five are extant genera (*Monachus*, *Leptonychotes*, *Lobodon*, *Ommatophoca*, and *Hydrurga*) and four fossil (*Pristiphoca*, *Paleophoca*, *Monotherium*, and *Pontophoca*); and three to Cystophorinae, of which two are extant genera (*Cystophora* and *Mirounga*) and one fossil (*Mesotaria*).

The total number of extant species in the family is 18: eight belong to the subfamily Phocinae (six in genus *Phoca* and two in the monotypical genera *Halichoerus* and *Erignathus*), seven to Monachinae (three in genus *Monachus*, the rest in the above-listed monotypical genera), and three to Cystophorinae (*Cystophora cristata* and two species in genus *Mirounga*).

119 The Greenland harp seal (*Ph. groenlandica*), gray seal (*Halichoerus grypus*), hooded seal (*Cystophora cristata*), and the aegialoid (pagophobic) form of the common seal (*Ph. v. vitulina*) inhabit only the basin of the North Atlantic and the adjoining portions of the Arctic Ocean; the Mediterranean monk seal (*Monachus monachus*) inhabits the subtropical sections, especially the North African and Mediterranean coasts; and the Caribbean monk seal (*Monachus tropicalis*) inhabited the Caribbean Sea.

The following three species of this family are found in the North Pacific Ocean: the Hawaiian monk seal (*Monachus schauinslandi*), ribbon seal (*Phoca fasciata*), and two forms of the common seal (*Ph. vitulina*), i.e., pagophilic (*Ph. v. largha*) and pagophobic (*Ph. v. kurilensis*). The latter two species partly penetrate the Chukchi Sea also. Moreover, the northern elephant seal (*Mirounga angustirostris*) is encountered along the American coast. *Phoca hispida* and *Erignathus barbatus* are common to the basin of the North Atlantic, seas of the North Arctic Ocean, and the northernmost and northeastern parts of the Pacific Ocean. The common seal, absent in the Arctic Ocean (with the exception of the coastal waters of Murman), thus enjoys a typical amphiboreal range. Two species of

the genus *Phoca* (*Ph. caspica* and *Ph. sibirica*) inhabit the landlocked reservoirs of the Old World—the Caspian Sea and Lake Baikal.

Four species of eight-incisored seals (*Lobodon carcinophaga*, *Lep-tonychotes weddelli*, *Ommatophoca rossi*, and *Hydrurga leptonyx*) and the southern elephant seal (*Mirounga leonina*) inhabit the Southern hemisphere, mainly around Antarctica (in the notopelagic zone).

Many species of the family are of considerable economic importance as valuable sources of fur, skin, blubber, and meat (for the state animal farms).

One species (*Hydrurga leptonyx*) is a predator inflicting damage on penguins and most other species of antarctic seals on which it survives. Many seal populations of the genera *Monachus* and *Mirounga* have suffered greatly as a result of rapacious hunting.

The fauna of the USSR contains (with the proviso stated on p. 502) all the three subfamilies and the five genera. Three of the latter belong to the ten-incisored seals (Phocinae—*Phoca*, *Halichoerus*, and *Erignathus*), one to the subfamily of hooded seals and elephant seals (Cystophorinae—*Cystophora*), and one to the subfamily of monk seals (Monachinae—*Monachus*). These five constitute 50% of the genera in the family. The total number of species of the family in our fauna is 10,¹⁶ i.e., 55% of the total number in the family. This constitutes about 3% of the number of species in the USSR fauna. The range encompasses all our territorial waters and the adjoining pelagic expanses.

Two species belonging to the subfamilies Monachinae and Cystophorinae represent rather chance elements of our fauna. One of them, the Mediterranean monk seal (*Monachus monachus*), became totally extinct in the USSR waters of the Black Sea by the early twentieth century and its casual finds on our coasts represent an exceptional rarity from the Bulgarian or Anatolian populations whose numbers are insignificant. Another species, the hooded seal (*Cystophora cristata*), though not a regular find, is nevertheless fairly frequent, usually singly, in the northernmost regions of the White Sea or in the adjoining sections of the Barents Sea. Barring these two species (genera), there is only one Soviet subfamily and the number of Recent genera of true seals in our fauna is only 33% of the total number of genera of true seals in the world fauna; the number of living species, however, constitutes about 45% of their total number. Of the total number of species in our mammalian fauna, the number of Pinnipedia of the family Phocidae known in the USSR is 2.6%. The range of the family, not including the monk seal, covers the entire territorial waters of the USSR except the Black Sea.

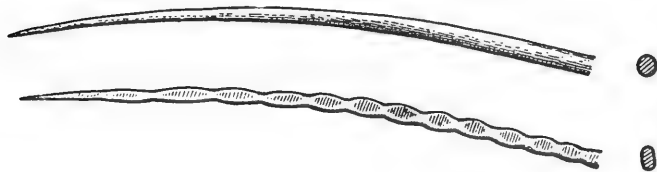
¹⁶ Combining *Phoca vitulina* and *Ph. largha* into a single species.

- 120 All the other species of the family, apart from the elephant seals and the eight-incisored seals of the Southern hemisphere, are represented in our fauna and, except for the two Atlantic species (*Ph. vitulina* and *Halichoerus grypus*), are of great importance in the field of game hunting. (K. Ch.)

Key to Species of True Seals (Phocidae)

Identification Based on External Features

- 1 (16). Upper incisors six (three on each side of jaw). Claws well developed on fore as well as hind flippers.
- 2 (3). Whiskers slightly flattened, smooth (Fig. 81). Fore flippers short and broad, with almost transversely incised anterior margin; middle digit (with claw) perceptibly longer than rest. Color fairly monochromatic, sometimes with dull spots. Dimensions large: body length of adult not below 200 cm. Two pairs of teats. Bearded seal, *Erignathus barbatus* (pp. 166-211)
- 3 (2). Whiskers highly flattened, with wavy edges. Fore flippers relatively long, with obliquely incised anterior margin. Length of first two digits (with claw) longer than third. Coloration of different types. One pair of teats.
- 4 (5). Head with long and high snout. Upper contour of its profile straight or even convex on the nose bridge. Cheek teeth [post-canines] quite large and generally with a single cusp. Color dull and spotted, brighter on breast and flanks than on back. Body length of adults in a straight line over 150 cm. Gray or long-snouted seal, *Halichoerus grypus* (pp. 454-495)
- 5 (4). Head with moderately long, low snout. Upper contour of its profile with fairly distinct small break in anterior portion of forehead (on nose bridge). Crowns of cheek teeth, especially of



120 Fig. 81. Structure of the cheek whiskers of seals. Above—smooth whiskers of the bearded seal; below—more flattened whiskers with wavy edges in the rest of the true seals (figure by K.K. Chapskii).

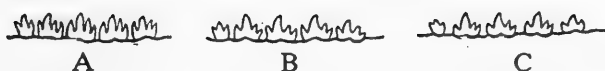
lower ones, with additional cusps set in front and back of main tooth. When the anterior cusp is absent on lower teeth, main cusp is not pointed and teeth in general are relatively small. Color and dimensions vary. Body length not above 150 cm.

- 6 (13). Color of hair coat usually dark and spotted, dorsally with fairly sharp light-colored streaks or speckled, or altogether monochromatic, dark.
- 7 (8). Teeth relatively massive. Majority of lower cheek teeth with longitudinally elongated crown; cheek teeth in relation to general row of teeth often set obliquely; accessory cusps somewhat inclined toward the middle (main) cusp, with which bases merge (Fig. 82). Color of hair coat spotted, with light-colored streaks, or speckled with light-colored background. Body length of adults in a straight line not less than 140 cm. Common seal, *Phoca vitulina* (pp. 307-369)¹⁷
- 8 (7). Teeth not large, relatively thin. Lower cheek teeth usually with highly disjointed crown, accessory cusps not inclined toward the base (Fig. 83). Color of hair coat dorsally monochromatic or spotted, with or without light-colored streaks. Body length in a straight line less than 140 cm.
- 9 (10). Cheek teeth with vertically disposed high accessory cusps. Color monochromatic. Light-colored gaps or dark-colored spots absent. Baikal seal, *Phoca sibirica* (pp. 290-306)
- 10 (9). Cheek teeth with accessory cusps directed forward and backward (fanlike). Color of skin not monochromatic, with pattern.
- 11 (12). Color of skin with dark main background of back (ventral side often paler), interrupted by light-colored streaks for the most part in form of whole or broken lines. Ringed seal, *Phoca hispida* (pp. 218-260)
- 12 (11). Color of skin variegated, dove-gray, dorsally mainly with light-colored streaks but rarely assuming shape of closed rings, with innumerable spots of diverse sizes and shapes, dark and sometimes almost black, and scattered haphazardly. Caspian seal, *Phoca caspica* (pp. 260-290)



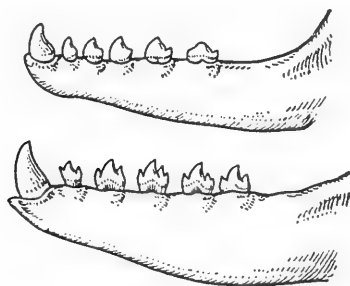
121 Fig. 82. Structure of the crowns of upper and lower cheek teeth of the common seal, *Phoca vitulina* (figure by K.K. Chapskii).

¹⁷See note at the end of this Key.



121 Fig. 83. Structure of the crowns of lower (cheek) teeth in the small species of the genus *Phoca*. A—Baikal seal, *Ph. sibirica*; B—ringed seal, *Ph. hispida*; C—Caspian seal, *Ph. caspica* (figure by K.K. Chapskii).

- 13 (6). Large light-colored, almost white sections alternate with dark brown, often nearly black sections in hair coat of adults. Color of young ones not intensely spotted or altogether without spots, dull gray; in animals of transitional age, young and adult, rudiments of above pattern seen vaguely (like a shadow). Light-colored streaks totally absent in all stages.
- 14 (15). Adults with well-defined (or diffused at edges) large dark-colored, paired wing-shaped patches that stand out prominently against light-colored background dorsally along flanks. Young animals gray, with haphazardly scattered, large (angular) and minute spots. Lower cheek teeth (apart from the first) with well-developed accessory cusps and pointed main cusp (Fig. 84).
 Greenland seal, *Phoca groenlandica* (pp. 369-436)
- 122 15 (14). Adults with four light-colored closed bands against dark-colored background: around neck, around base of fore flippers, and in lumbar portion. In young animals dorsal side dull brown, with distinct boundaries of dark field at site of future bands. Lower cheek teeth small, with poorly developed accessory cusps (often only one) and obtuse main cusp.
 Ribbon seal, *Phoca fasciata* (pp. 436-454)



122 Fig. 84. Form of teeth crowns in the lower jaw. Bottom—Greenland seal, *Phoca* (*Pagophilus*) *groenlandica*; above—ribbon seal, *Phoca* (*Histiophoca*) *fasciata* (figure by K.K. Chapskii).

- 16 (1). Upper incisors four (two on each side of jaw); color either dull and dark or bright and spotted.
- 17 (18). Lower incisors four (two on each side of jaw). Cheek teeth extremely massive, often set obliquely toward general line of tooth row. Color dull, brown, sometimes with large, nearly rectangular patch in lower half of body. Whiskers smooth. Two pairs of teats. Mediterranean monk seal, *Monachus monachus* (pp. 502-515)
- 18 (17). Lower incisors two (one in each half of jaw). Crowns of cheek teeth not large. Color of main background gray, covered with rather rare, irregularly shaped, nearly black patches. Whiskers flattened, with wavy edges. One pair of teats. Hooded seal, *Cystophora cristata* (pp. 524-547) (K. Ch.)

Identification Based on Skull Features

- 1 (16). Three incisors on each side of upper jaw (total of upper and lower incisors 10). Lateral contours of rostral part of skull, viewed from above, reveal perceptible convexity anterior to orbits (Fig. 85).
- 2 (3). Alveoli of upper incisors with circular opening. Zygomatic bones greatly reduced and broad, their smallest length (without processes) exceeding smallest width by not more than 1.5 times and smaller than interorbital space. Cheek teeth (when not worn) with poorly developed accessory cusps, firmly fused with main cusp. Tympanic bullae flattened; their outline viewed from

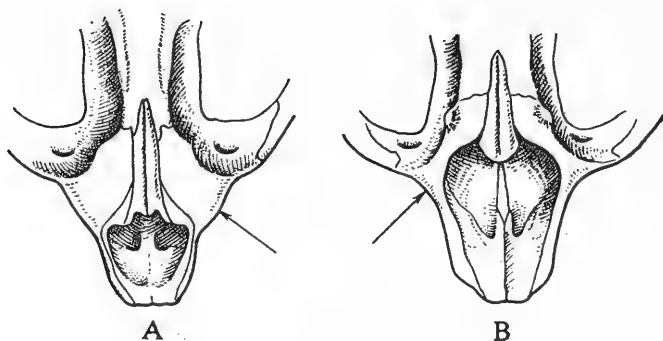


Fig. 85. Rostral-facial part of the skull of seals. A—ribbon seal, *Phoca (Histriophoca) fasciata* (lateral contours with convexity); B—hooded seal, *Cystophora cristata* (concave lateral contours) (figure by K.K. Chapskii).

- below resembles a trapezoid.
 Bearded seal, *Erignathus barbatus* (pp. 166-211)
- 3 (2). Alveoli of upper incisors distinctly compressed laterally. Smallest length of zygomatic bones (without processes) more than 1.5 times their smallest width and more than interorbital width. Cheek teeth with or without well-developed accessory cusps. Tympanic bullae sharply convex and, viewed from below, reveal more or less oval outline.
- 4 (13). Lower posterior process of zygomatic bone considerably longer than upper. Posterior edge of bony palate with deep arcuate or angular notch. Bony septum in internal nares does not extend beyond two-thirds of longitudinal suture between palatine bones.
- 5 (6). Skull, viewed from above, does not reveal infraorbital foramen, which is concealed by carinate crest on orbital side of zygomatic process of upper jaw (Fig. 86). Crowns of most cheek teeth of upper jaw with single cusp (without accessory cusps posteriorly). Upper contour of skull profile straight; anterior portion of skull in zone of nasal bones in adults almost as high as occipital portion. Outline of nasal opening [nares] perceptibly broadened in upper part (Fig. 87).
 Gray or long-snouted seal, *Halichoerus grypus* (pp. 454-495)
- 6 (5). Sharp carinate crest absent on anterior wall of orbit and infraorbital foramen distinctly visible. Crowns of cheek teeth (except the first) with additional cusps (at least one posterior to the main). Upper contour of skull profile appears as a convex line;

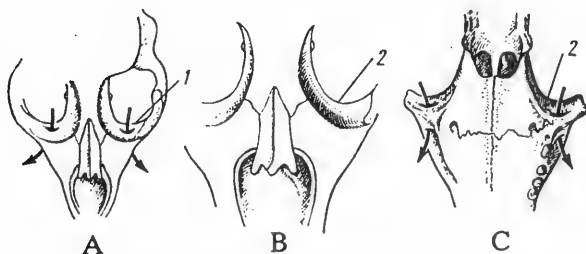
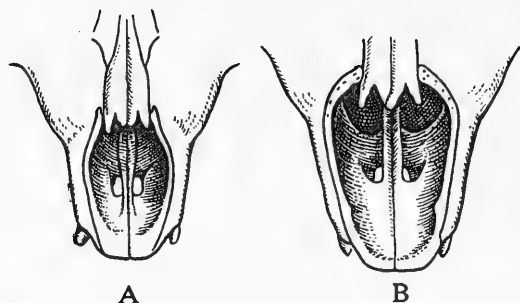


Fig. 86. Position of the infraorbital foramen. A—seal of the genus *Phoca*; B and C—gray seal, *Halichoerus grypus*: 1—anterior lower edge of orbits in all seals of the genus *Phoca* s. lato; 2—crest. Infraorbital foramen (shown by arrow) in seals of the genus *Phoca* viewed from above and in the gray seal covered from above by crest (B) and seen only from lower side (C) (figure by K.K. Chapskii).



123 Fig. 87. Contour of nostril. A—larga, *Phoca vitulina* [*largha*]; B—gray seal, *Halichoerus grypus* (figure by K.K. Chapskii).

facial part, even among adults, perceptibly below the occipital. Contour of upper part of nares not more broadened than middle and lower parts.

- 124 7 (8). Teeth relatively large; longitudinal diameter of alveolus of canine and narrowest part of interorbital space (from above) exceed maximum width of infraorbital foramen. Most of lower cheek teeth with longitudinally elongated crown, quite massive at base and not deeply divided; all cusps closely fused with bases while accessory cusps are inclined toward the main. Cheek teeth often set obliquely in relation to general line of tooth row (Fig. 82). Common seal, larga, *Phoca vitulina* (pp. 307-369)¹⁸
- 8 (7). Teeth relatively small; longitudinal diameter of alveolus of canine and narrowest part of interorbital space less than width of infraorbital foramen. Lower cheek teeth not massive but with relatively high and deeply cloven crown; their accessory cusps not inclined toward the main cusp; set straight in relation to general tooth row.
- 9 (10). Tympanic bullae small and widely set, their length less than gap between them. Bony lobe of external auditory meatus narrow: its width less than gap separating it from crest of articular fossa (Fig. 88). Length of rostral part of skull exceeds length of orbits (Fig. 89). Caspian seal, *Phoca caspica* (pp. 260-290)
- 10 (9). Tympanic bullae more or less large; their length not less than gap between them. Bony lobe of external auditory meatus wider than gap separating it from crest of articular fossa. Length of rostral part of skull less than length of orbit.

¹⁸ See note at the end of this Key.

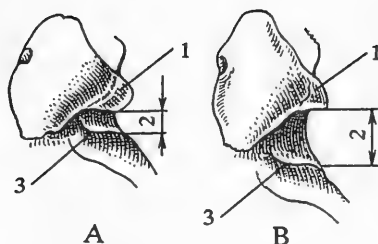


Fig. 88. Bony lobe of external auditory meatus (1) and gap (2) between it and crest of the articular fossa (3). A—ringed seal, *Phoca hispida*; B—Baikal seal, *Ph. sibirica* and Caspian seal, *Ph. caspica* (figure by K.K. Chapskii).

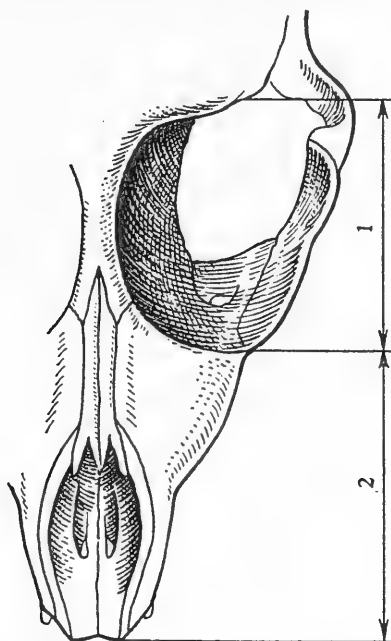


Fig. 89. Ratio between length of the orbit (1) and length of the rostral (preorbital) part of the skull (2) in the Caspian seal, *Phoca caspica* (figure by K.K. Chapskii).

- 11 (12). Lower cheek teeth closely set, with high, nearly parallel (like crests) accessory cusps (Fig. 83, a). Anterior edge of nasal bones without median projection. Length of tympanic bullae roughly equal to gap between them or slightly more.
 Baikal seal, *Phoca sibirica* (pp. 290-306)
- 12 (11). Lower cheek teeth (except the first) with deflected (fanlike) anterior and posterior cusps, considerably shorter than middle

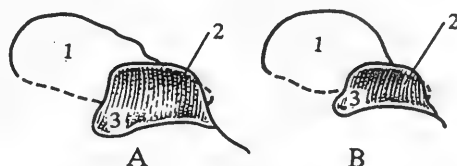
- 125 (main) one. Anterior margin of nasal bones with median projections. Length of tympanic bullae perceptibly more than gap between them. Ringed seal, *Phoca hispida* (p. 218)
- 13 (4). Lower posterior process of zygomatic bone not longer than upper posterior. Posterior edge of bony palate without deep notch. Bony septum in internal nares can extend far backwards, even up to posterior edge of palate.
- 14 (15). Lower cheek teeth (except the first) relatively large, with well-developed acute cusps anterior and posterior to the main one, which is also pointed (Fig. 84, a). Posterior edge of bony palate without notch in midportion, sometimes with posterior projection. At least base of bony septum in choanae reaches posterior edge of bony palate. Tympanic bullae not bent (Fig. 162). Their external auditory meatus geniculately bent forward. Greenland seal, *Phoca groenlandica* (pp. 369-436)
- 15 (14). Lower cheek teeth small, with obtuse rounded main cusp and poorly developed accessory cusps, of which anterior one generally absent. Posterior edge of bony palate faintly notched, usually in form of shallow braces. Compact bony septum in choanae rarely reaches posterior edge of palate. Tympanic bullae strongly bent (Fig. 178). External auditory meatus not geniculately bent. Ribbon seal, *Phoca fasciata* (pp. 436-495)
- 126 16 (1). Two incisors in each half of upper jaw (upper and lower incisors not more than eight). Lateral contours of rostral part of skull, viewed from above, concave anterior to orbits (Fig. 85).
- 17 (18). Two incisors on each side of upper and lower jaws (eight incisors in all). Nasal processes of premaxillary bones reach nasal bones. Longitudinal bony septum in internal nares does not reach posterior margin of bony palate, which has a sharp notch. Posterior lacerate foramen far short of reaching basal suture. Mediterranean monk seal, *Monachus monachus* (pp. 502-519)
- 18 (17). One incisor on each side of lower jaw (six incisors in all). Nasal processes of premaxillary bones far short of reaching nasal bones. Longitudinal bony septum in internal nares reaches end of bony palate, which has no notch. Posterior lacerate foramen extends far anteriorly, almost up to basal suture (Fig. 85): Hooded seal, *Cystophora cristata* (p. 524). (K. Ch.)

Note: There is a view (Chapskii, 1967, 1969) that the Pacific Ocean populations of the common seal, *Phoca vitulina*, usually regarded as a subspecies, represent, in fact, two independent species: one, the conspecific Atlantic, i.e., the common seal (*Ph. vitulina*) and the other the specific

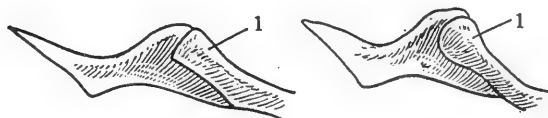
Pacific species, i.e., the seal associated with ice floes or the "pagophilic" larga (*Ph. largha*). This aspect calls for further investigation. In this book, however, the prevailing broader interpretation of the species *vitulina* (q.v.) has been adopted. The following are the main features distinguishing the two groups of seals:

a) Transverse profile of tympanic bulla with high and fairly steep curvature toward the base of the lobe of the external auditory meatus (Fig. 90); fork of the posterior edge of the zygomatic bones arcuate (Fig. 91); nasal processes of the premaxillary bones adjoin the nasal bones over a considerable distance (Fig. 92). Posterior edge of the bony palate usually arcuate (Fig. 93). Color of skin variegated: either gray with whitish, often annular streaks and numerous dark spots or dabs, or brightly speckled with light colored underside. . . . Larga, ***Phoca largha***

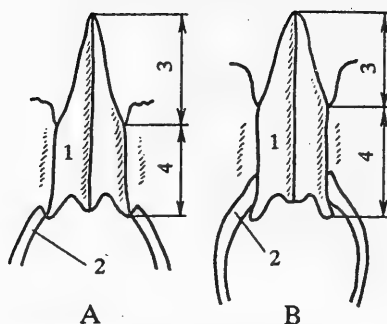
b) Transverse profile of tympanic bulla with low steplike interruption toward the base of the lobe of the external auditory meatus (Fig. 90); fork of the posterior edge of the zygomatic bones in the form of an angle (Fig. 91); nasal processes of the premaxillary bones only just barely or do not reach nasal bones (Fig. 92). Posterior edge of bony palate usually in the form of braces or an angle (Fig. 93). Color of the skin darker, with spots and clear spaces. . . . Common seal, ***Phoca vitulina***. (K.Ch.)



125 Fig. 90. Transverse contour of the tympanic bulla (1) and bony lobe of the external auditory meatus (2) partly covered by the articular fossa (3) in different forms of the common seal, *Phoca vitulina*, as seen in the lower part of the upturned skull anteriorly (figure by K.K. Chapskii). A—pagophobic forms of the common seal: Atlantic, *Phoca v. vitulina*; Kuril (Island), *Ph. v. kurilensis*; Richard's, *Ph. v. richardi*; B—pagophilic form of seal: Far-Eastern larga, *Ph. v. largha*.



125 Fig. 91. Articulation of zygomatic bone with zygomatic process of temporal bone (1): angular notch on the posterior edge of the zygomatic bone in the pagophobic form, *Ph. v. vitulina*, and arcuate in pagophilic form (larga), *Ph. v. largha* (figure by K.K. Chapskii).



125 Fig. 92. Nasal and premaxillary bones in different forms of the common seal, *Phoca vitulina*. A—Atlantic common seal, *Ph. v. vitulina*; B—largha, *Ph. v. largha* (figure by K.K. Chapskii): 1—nasal bone; 2—premaxillary bone; 3—facial part of nasal bone; 4—maxillary part of nasal bone.

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Subfamily of True, or 10-incisored, Seals

Subfamily PHOCINAE Gill, 1866¹⁹

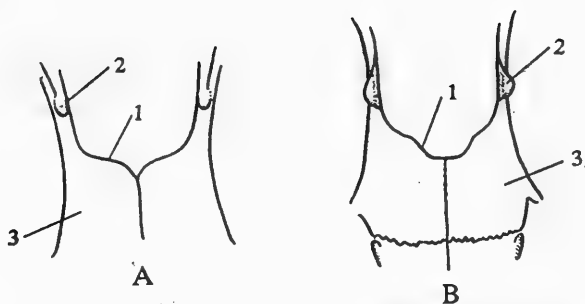
These are large-, moderate-, or small-sized seals. Body length [in adults] including the tail along the dorsal curvature (L_c) varies from 100 to almost 300 cm.

The hind flippers are longer than the fore flippers and both possess well-developed claws. On the fore flippers the third digit is somewhat shorter than the two preceding ones; it is noticeably longer than all the rest only in one species (bearded seal, *Erignathus barbatus*). A proboscis-like growth is absent in the anterior upper portion of the snout. The whiskers are usually highly flattened, with wavy edges; they are smooth and slightly compressed only in one genus (bearded seal).

The teats are one pair, except in the bearded seal in which there are two pairs.

The skull is usually not particularly large and is highly compressed between the orbits which, in most of the species, with rare exceptions, are very large. The maxillary bones directly anterior to them bulge markedly.

¹⁹ Strictly speaking, Gray (1825, 1850, 1866) enjoys the priority of classifying the true seals (Phocidae) into subfamilies as also of establishing the subfamily Phocinae. He designated this subfamily as "Subfamily 2. Phocina". His error in formulating this subfamily, i.e., inclusion of the walrus in it, was not an exception among the works of that time. Thus, Gill (1866), to whom the formal priority was assigned for the classification of the subfamily, Simpson (1945), and Scheffer (1958) also committed an error by including the monk seal in the subfamily (K. Ch.).



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Fig. 93. Structure of the palato-choanal region in different forms of the common seal, *Phoca vitulina*. A—Atlantic common seal, *Phoca v. vitulina*; B—largha, *Phoca v. largha* (figure by K.K. Chapskii): 1—contour of the posterior margin of the bony palate; 2—uncinate process of the pterygoid bone; 3—horizontal part of the palatine bone.

The preorbital processes are absent or highly reduced. The outer edge of the external auditory meatus, with the exception of the genus *Erignathus* (bearded seal), terminates with a bony lobe or is differently structured (Greenland [harp] seal, *Phoca groenlandica*). The anterior edge of the nasal bones is dentate and, when the median prominence is absent, without an inverted angular notch. The nasal processes of the premaxillary bones adjoin the nasal bones and are usually wedged between them and the upper maxillary bones or, in a few cases (gray seal, *Halichoerus grypus*, and to a lesser extent in the pagophobic members of the subgenus *Phoca* s. str.), slightly short of reaching them. The posterior lacerate foramen with one exception (genus of bearded seals, *Erignathus*), extends considerably forward along the inner side of the tympanicum.

There are three incisors in the upper jaw and two in the lower jaw on each side. The dental formula is:

$$I \frac{3}{2}, C \frac{1}{1}, P \frac{4}{4}, M \frac{1}{1} = 34.^{20}$$

The crowns of the cheek teeth when worn down, with one exception (gray seal, genus *Halichoerus*), with well-developed accessory cusps while these teeth (except for the first premolar) have two roots in most of the species (except in the foregoing genus and also quite often in the ribbon seal, subgenus *Histiophoca* of genus *Phoca*).

The postnatal hair coat is usually of the "embryonic" [lanugo] type, with dense, long fur, and is shed toward the end of lactation. Among

²⁰ Sometimes a second molar is seen.

the pups of the pagophobic members of the subgenus of ringed seals, *Phoca* s. str. (genus *Phoca*) and the bearded seal (genus *Erignathus*), the embryonic coat is shed in the mother's womb itself just before birth. In the former case it is white (or creamy) and in the latter, brownish-gray.

Most of the forms are pagophilic but some (gray seal, genus *Hali-choerus*, and the pagophobic form of the subgenus *Phoca* s. str., genus *Phoca*) whelp and molt on land.

- 129 Food specialization is not particularly distinct: it is most pronounced in bearded seals, genus *Erignathus* (benthic feeders) and *Phoca sibirica* (consuming mainly gobies and sculpins (Baikal oil-fish)) but specialization is not complete even among them.

These animals are distributed in the cold and moderate belts of the North Atlantic and North Pacific oceans, in the Arctic Ocean, and also in some landlocked water bodies of the Old and New World (Fig. 94).

Phocinae, with several features of a more primitive nature still preserved, apparently evolved earlier than the other subfamilies. Although their oldest finds date back to the Upper Miocene, the actual appearance of the group Phocidae should be placed in a much earlier period, perhaps the Early Miocene or even Oligocene. The following arguments indirectly support this view.

Firstly, even much earlier finds of Phocidae are known but presumably placed among Cystophorinae (see p. 262).

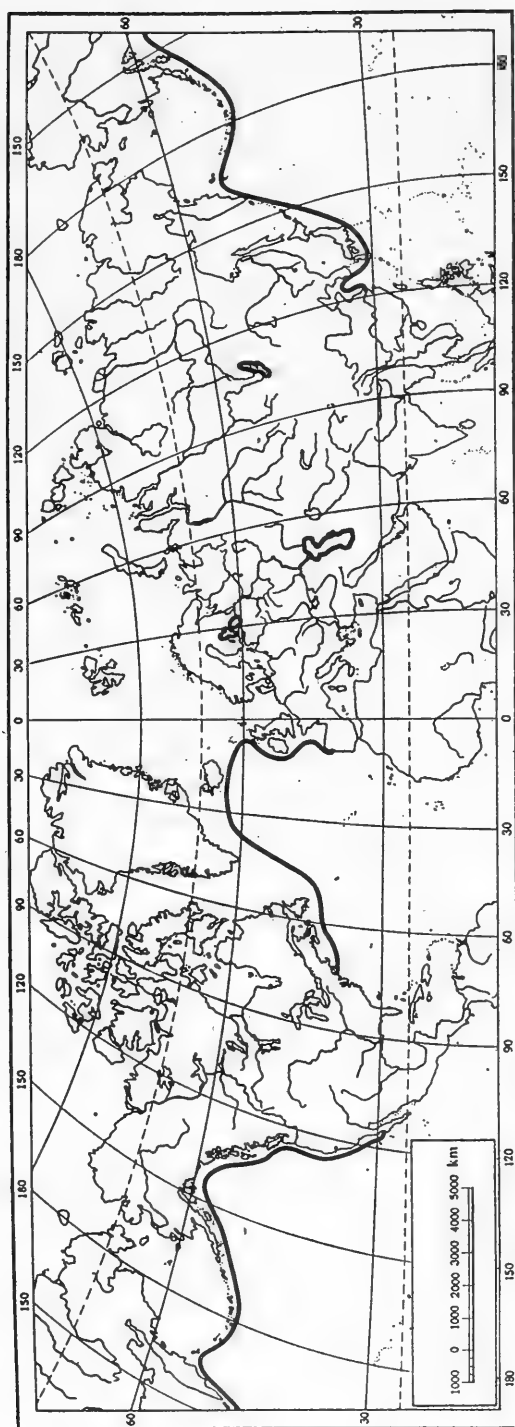
Secondly, the fossil finds of Phocinae from the Sarmatsk formations (Upper Miocene) represent the fully developed forms of the subfamily.

Thirdly, eight-incisored seals coexisted with them (see p. 498); the former could not have evolved simultaneously with the Phocinae.

The landlocked water bodies, i.e., the seas of the Old World, somewhere in the Tethys and its sources, could perhaps be regarded as the zone of evolution of the Phocinae.

By the beginning of the present century the system of the subfamily was quite well established but became the subject of dispute in the mid-1960s. The debate centered around the suggestion that the members of the subfamily of hooded seals or the 6-incisored seals (Cystophorinae) be included in it and doubts as to the affinity of the genus of bearded seals, *Erignathus*, to this subfamily (King, 1966).²¹ Evidently, the classic interpretation of the subfamily has been favored (see p. 148).

²¹ The karyotype of the bearded seal ($2n = 34$, $NF = 66$) is well distinguished from that of the Baikal (*Ph. sibirica*), Caspian (*Ph. caspica*), and Greenland (*Ph. groenlandica*) seals ($2n = 32$, $NF = 62$). It coincides with the karyotype of Weddell's seal (*Leptonychotes weddelli*) from the subfamily of monk seals, Monachinae (Anbinder, Mlekopitayushchie [Mammals], Novosibirsk, 1970) (V.H.).



128 Fig. 94. Reconstructed range of the subfamily of 10-incised seals, Phocinae, showing the southern boundary (K.K. Chapskii).

The subfamily comprises 10 genera (45.5% of the total number of genera in the family) of which seven are extinct and three extant (about 14% of all the extant genera of the family): *Phoca* Linnaeus, 1758; *Erignathus* Gill, 1866; and *Halichoerus* Nilsson, 1820. The total number of extant species is 8, which constitutes 44.5% of the total number (18) of the Recent species of the family.

The economic importance of the subfamily is significant. Some species (Greenland [harp] seal, *Phoca groenlandica*, ringed seal, *Ph. hispida*, and Caspian seal, *Ph. caspica*) form the basis of the marine-game industry. Their importance is primarily due to the fact that these animals are concentrated in large numbers in some seasons, making it possible to collect large quantities of hides of high commercial value (from which furs of various types are produced) as also other raw materials (blubber and meat for animals).

Three genera (100% of the genera of the subfamily) with 8 species (100% of the species of the subfamily) are found in the USSR. These are distributed in all the seas surrounding our country, except the Black Sea, and in some landlocked water bodies such as Lakes Ladoga and Baikal and the Caspian Sea. All the species, especially the Greenland and Caspian seals, are of commercial importance. (K. Ch.)

Genus of Bearded Seals

Genus *Erignathus* Gill, 1866

1866. *Erignathus*. Gill. Proc. Essex. Inst., 5: 5, 9. *Phoca barbata* Fabricius
= *Phoca barbata* Erxleben.

These are seals of large dimensions with a massive trunk, relatively small head, and a somewhat shortened neck.

The snout is moderately stretched, the eyes are relatively small, and a narrow fringe of bare skin is seen around the nostrils. The extremely fluffy upper lip has abundant (over a hundred) long, thick, smooth whiskers (without wavy edges). The hand has a very long middle digit, protruding noticeably farther than the rest.

The skull has a spacious cranium, relatively small orbits, and poorly developed zygomatic arches. The interorbital area is not highly compressed and the rostral part is broad. The zygomatic bones are sharply reduced and broad; the length of the bone without the processes is only slightly more (not more than 1.5 times), or even does not exceed, its smallest width. The tympanic bullae, viewed from below, appear nearly trapezoidal, with a distinct inner posterior angular projection in which

the carotid foramen is disposed. The nasal processes of the premaxillaries reach the nasal bones and extend along them quite far behind their anterior edge. A longitudinal bony septum in the internal nares (within the palatine bones) is absent.

The dental formula, as in other seals of the subfamily, is:

$$I \frac{3}{2}, C \frac{1}{1}, P \frac{4}{4}, M \frac{1}{1} = 34.$$

The upper incisors have fine roots, circular in cross section; their alveoli are also correspondingly circular in cross section. The crowns of the premolars and molars, excluding the initial ones, have one (posteriorly) or two (anteriorly and posteriorly) obtuse accessory cusps (Fig. 95). With the exception of the first premolar, all the cheek teeth have two weak roots which are set apart. The teeth wear out and fall out early.

The body is rather monochromatic although the underside is usually somewhat lighter than the upper; young animals have fine spots. The primary, prenatal pelage is not of the embryonal type but cinnamon-brown (sometimes incompletely) just before the pup is born. Age-related changes are minor and mainly manifest in body size and partly in coloration, as well as in the structure and proportions of the skull. Sexual dimorphism is negligible.

Two pairs of teats are present.

These seals are biologically associated with ice floes on which they reproduce and molt and also with shallow waters since they feed mainly on benthic invertebrates. They do not form large groups on ice floes. Migrations do occur but are not very distinct. Mating does not involve the formation of harems and there are no special fights among the adult males.

The animals are distributed in the circumpolar region in the seas with an arctic regime and inhabit the periphery of the Arctic Ocean,

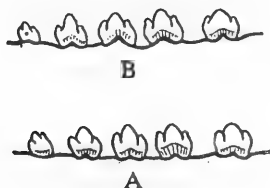


Fig. 95. Structure of the crown of undamaged lower teeth in a young bearded seal, *Erignathus barbatus*. A—from the inner side; B—from the outer side (figure by K.K. Chapskii).

northern edge of the Atlantic Ocean, and the northwestern part of the Pacific Ocean (Bering Sea and the Sea of Okhotsk).

131 Among the 10-incisored seals, the genus *Erignathus* occupies a special position. Several morphological characters preserving features of relative primitivity, to some extent the result of adaptation to benthic feeding, prompted the inclusion of this genus under a distinct monotypic tribe, Erignathini (Chapskii, 1955). The taxonomic independence is confirmed by data from serological investigations (V.I. Borisov) as also by cytogenetic data (the diploid chromosome number in bearded seals is $2n = 34$ and in Phocinae, $2n = 32$). Both these criteria compel us to place the genus *Erignathus* somewhat away from the rest of the 10-incisored seals in spite of considerable antigenic and cytogenetic similarity. At the same time, its genetic relation with other members of the subfamily are not yet quite clear. It is not clear to which genera of Phocinae *Erignathus* is most closely related. It is only evident that its predecessors separated from the main branch of true seals very long ago. Whether or not the genus *Erignathus* serves to some extent as a link for all the typical northern seals (Phocinae) in the same manner as the genus *Monachus* serves as the initial form for the formation of the typical (i.e., 8-incisored) seals of the Southern hemisphere is very difficult to state; the origin of the genus beyond the Pliocene has not yet been traced. Its phyletic lineage derives from the Pliocene form *Platyphoca* of the Belgian formations.

The North Atlantic basin is evidently the center of origin of the genus. The ratio between the extinct and extant species is 1:1.

The genus includes only one species, the bearded seal, *Erignathus barbatus* (Erxleben, 1777).

The range of the genus in the USSR evidently encompasses the whole of the Arctic and the Far Eastern seas (north of the Sea of Japan).

This species is of much importance as a target of hunters, at the same time posing no danger to the fishing industry. (K. Ch.)

BEARDED SEAL

Erignathus barbatus (Erxleben, 1777)

- 1776. *Phoca barbata*. Müller. Zoologiae Danicae prodromus. Nomen nudum.
- 1777. *Phoca barbata*. Erxleben. Systema regni animalis. I, p. 590. Waters of southern Greenland (Ognev, 1935).
- 1778. *Phoca leporina*. Lepechin. Acta Acad. Scient. Imper. Petropolitanae. I, p. 264, Tab. 8, White Sea.

1811. *Phoca nautica*. Pallas. Zoographia Rosso-Asiatica, I, p. 108. Sea of Okhotsk.
1811. *Phoca albigena*. Pallas. Ibid., p. 109. Kamchatka.
1817. *Phoca lachtac*. Desmarest. Now. Dict. Sc. Nat., 25, p. 581. Pacific Ocean.
1828. *Phoca parsonsii*. Lesson. Dict. Class. d. Hist. Nat., 13, p. 414. Northern seas. (V.H.)

Diagnosis

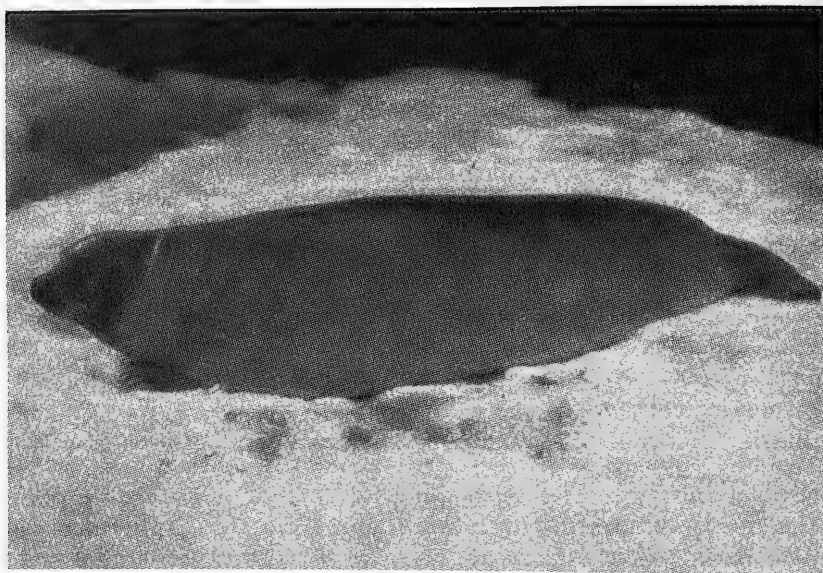
Only species of the genus.

Description

Body heavily built; head and flippers (especially the fore flippers), compared to body length and weight, are not very large (Fig. 96). The hands are short and broad as though truncated anteriorly. The fore flippers are markedly shifted forward and set relatively closer to the anterior end of the body than in other seals. Their claws are massive, with a quite
 132 distinct, transverse, age-related structure, i.e., ribbed. The whiskers are abundant, luxuriant, and set in 10 or 11 rows; five rows on the lower side have 11 to 18 whiskers each. Their total number on each side of the snout reaches 125.

The hair coat of the adult is perceptibly sparser than among other seals. In the young, however, it is dense and uniform, and the skin between the hairs is not visible. The structure of the hair coat is quite similar to that of other seals. Three categories of hairs are distinguish-
 133 able: guard, intermediary, and soft fur. Their quantitative ratios vary perceptibly with age. Among adults the hair coat consists 50% of guard hair, 30% of intermediary hair, and about 20% of fur. In pups, after shedding the embryonic pelage, the proportion of guard hair is less than 10%, intermediary hair slightly more than 40%, and the rest is fur (V.A. Potelov). The hair on the trunk is sparser and long but on the head, especially on the snout, it is short and dense; the nature of the coat on the flippers, especially on the hind flippers in the region of the ankle joint and on the extreme digits, is nearly similar.

The predominant color of the upper portion of the trunk is a brownish-gray or blackish-olive, gradually turning lighter, into light gray or dirty olive on the flanks and on the ventral side. Quite often, animals with a light and more monochromatic pale ash coloration, almost devoid of spots, are encountered. Along the median dorsal side, from head to tail, runs a barely visible narrow band with rather blunt edges, with a dark, sometimes almost black or slate-black coloration ("belt").



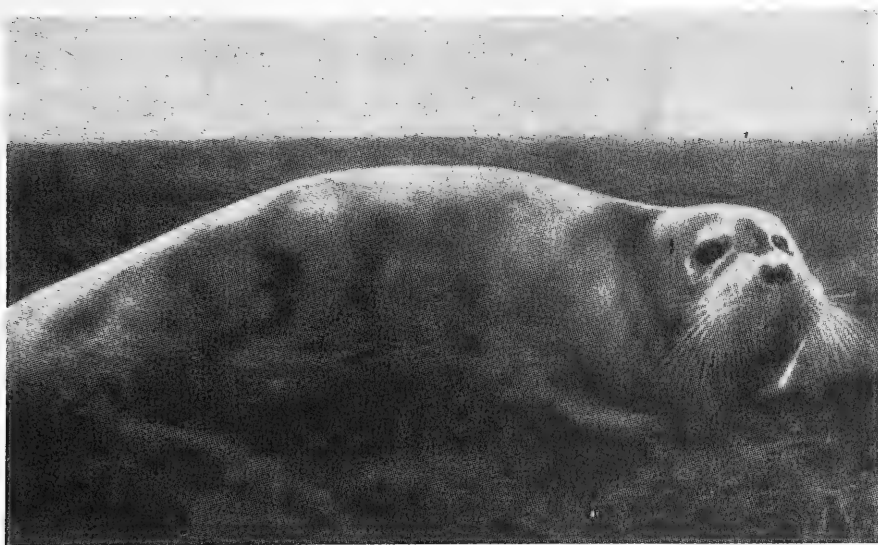
132

Fig. 96. Bearded seal, *Erignathus barbatus* (photograph by G.M. Kosygin).

Somewhat large but usually very indistinct dull whitish spots with fine uniform speckles against the background color are seen roughly from the level of the shoulder blades farther to the end of the body dorsally (Fig. 97). In some cases, mainly in adult animals, the spots are apparently very distinct and bright, sometimes almost white, devoid of variegation and distinctly visible from afar. Further, small dull spots, slightly darker than the main background, are visible in places. Though few, these spots catch the eye.

The head displays characteristic coloration in the form of whitish patches that are prominent in the overall dark gray or even gray background (Fig. 98). One very large patch is located on the sinciput [fore-head] and two pairs above the eyes and around the ear openings. The whiskers are light in color, mainly muddy-white. The claws are dark gray, almost black.

No color differences have been recorded in the hair coat between males and females. Age-related color changes have not been fully studied. The skin of newborn pups, compared to that of adults, is usually much darker, blackish-gray, sometimes light brown, with minor differences in color intensity between the upper and lower sides of the body. In most cases the flanks and the upper portions, more rarely the ventral side of the body, have numerous speckles, fused at places, usually



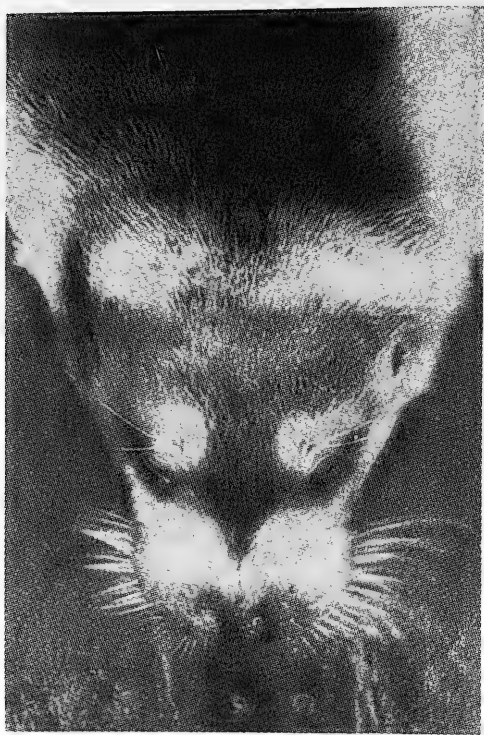
132 Fig. 97. Bearded seal. Devich'ya Luda Island, Kandalaksh Strait, White Sea, August, 1962 (photograph by V.D. Kokhanov).

more abundant in the anterior part of the body. They extend somewhat onto the head and fore flippers. The light-colored pattern on the head (sincipital and supraorbital spots and also the lighter parts on the lips) stands out contrastingly. The older juveniles and animals of transitional age gradually lose the speckled pattern and become more monochromatic in coloration, with warm brown shades somewhat more prominent. Sometimes the difference between the underside and the upper is smoothened but, nevertheless, the upper side is quite frequently dark-colored; a narrow dark band extending along the spine from the head to the tail is nonetheless visible. The color of adults is paler, monochromatic (but nevertheless usually more vivid on the spine), sometimes altogether light-colored, silvery-gray or pale olive. The pattern on the head becomes diffuse and almost disappears. Quite often, brownish, even rust-red tones appear around the head, on the throat, and on the neck.

134

Coloration is subject to considerable individual variation. The large light-colored spots on the trunk, tiny surface spots (dabs), and also the light-colored pattern on the sinciput appear differently in different animals. The vividness of the color of the dorsal and ventral sides likewise varies markedly.

In some specimens the dorsal whitish spots are barely visible while the granular dark speckles are widely scattered and sometimes even



133 Fig. 98. Color of the head of a five-year-old bearded seal. Barents Sea, May, 1963 (photograph by V.A. Potelov).

totally absent; in other animals they are brighter, sometimes unusually distinct and visible from a distance; they are also variable in size, disposition, number, and shape. The same is true of the spots/dabs on the sinciput. Their number, shape, distribution, and color are highly variable. Animals with no spots/dabs whatsoever are also encountered; in most animals, however, these are disposed along the body flanks and are absent ventrally, but specimens with a large number of ventral specks (appearing mottled as a result) are also encountered.

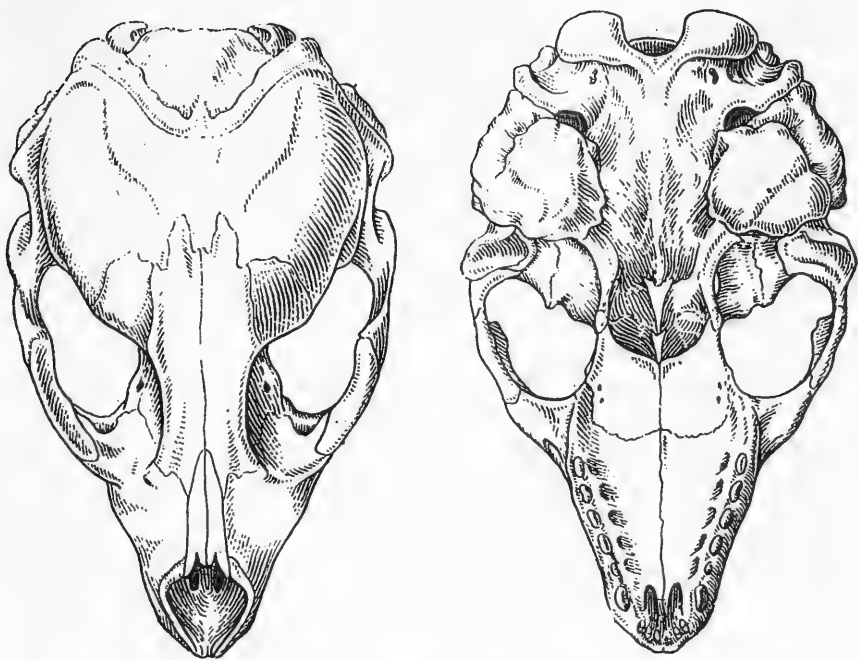
The color of the hair coat of adults evidently undergoes seasonal changes (fading). The color is a dark gray in autumn, gray in winter, and yellowish-gray in spring (V.A. Potelov).

The geographic variation in color is not well understood.

135 The skull features supplementing the generic craniological characteristics are as follows. Because of the small dimensions of the orbits and evidently the shortened zygomatic bones, the width at the zygomatic

arches usually does not exceed that of the cranium at the mastoid processes. The interorbital space is broad, without a sharp constriction, and flattened at the top; its width at the narrowest point is about one-fifth the mastoid width. The upper profile of the skull descends along a smooth S-shaped line from the apex of the nasal bones to the base of the nares.

The infraorbital foramina are large, vertically elongated, and their longer diameter slightly more than the longitudinal length of the alveolus of the upper canines. A longitudinal crest extends on both sides of the skull along the upper edge of the temporal bone; a notch is perceptible between this crest and the base of the zygomatic process (Fig. 99). The nasal bones are relatively broad; their posterior wedge-shaped end bears a round apex which is not sharply pointed while the anterior edge has long lateral projections between which a small, often slightly bifurcated, median projection is seen in most cases. At the point of juncture of the premaxillaries with the nasals, an angular notch is not formed on the upper posterior edge of the nares, which appear oval in shape from the front. The jugular processes are quite massive and bent backward sharply.



The posterior edge of the bony palate has a small, broad, slightly angular notch.

The upper tooth row has a sharp S-shaped curvature in the horizontal plane. The lateral (alveolar) edge of the upper jaw is sharply displaced downward like a crest. The upper premolars (except for the reduced first one) and the molar are usually without an anterior accessory cusp and mostly with a single posterior one. The corresponding lower teeth (except the first two) have two accessory cusps—one each anterior and posterior to the main cusp.

Sex-related differences in the skull are so insignificant that practically almost or no differences are seen in averages even in statistical variance analysis. Thus, while on the basis of the limited material of the 1930s (Chapskii, 1938) the condylobasal length of adult males from the Kara and Barents seas was 1.5 mm more than that of the corresponding values for females, this difference narrowed down to 0.7 mm with quantitatively more complete data (Potelov, 1968). Almost no difference was seen in the mastoid width (at the mastoid process) while the width of the rostrum in males exceeded the average corresponding value in females by only 1 mm. As a percentage of the mastoid width, the difference in width of the rostrum was slightly more noticeable: in males 36% and in females about 34%. Differences in other indices (height of forehead, length of forehead, and length of cranium) were insignificant. However, contrarily, indices of length of the nasal bones and skull height of females were slightly higher than those of males. There were no sex-related differences whatsoever in terms of percentages of condylobasal length (mastoid and rostral width, length of nasals, their width at base of the apex, etc.) (Potelov, 1968). According to other data (Ognev, 1935), the craniological differences between males and females were slightly more. But this statement is based on limited data since the sexwise analysis could not have been made at that time with the desired degree of accuracy.

The age-related changes of the skull conform to the general principles. In pups the skull is relatively inflated, the forehead stunted, and the rostral portion highly narrowed; the upper profile sharply dips forward and the interorbital space is relatively wider than in adults. With growth, the skull becomes more elongated due to the marked elongation of the forehead and the relatively less enlargement of the cerebral section. The index of the rostral width as a percentage of the mastoid increases from 30% among six-month-olds to 36% in adults, while the index of skull
136 height decreases from 72 to 64%. The age-related changes of the median bifurcated projection of the coronal suture are significant: this projection narrows and increases in length with age while its saddle-shaped notch becomes deeper and acute. Rapid wear and shedding of teeth is highly

typical. With advancing age, the skull becomes more massive, a feature associated with the thickening of the bones and also the elongation of the interfacial (longitudinal) suture relative to the interparietal length (Ognev, 1935; Chapskii, 1937).

The geographic variation of the skull, although manifest in some indices (Ognev, 1935; Naumov and Smirnov, 1936; Chapskii, 1963), calls for review based on a more comparable and wider series (see under "Geographic Variation," p. 181). Variation is perceptible in the total length, form of the nasal bones, width of the nares, and the interorbital space.

The os penis is very faintly curved and considerably more thickened than in the other 10-incisored seals. Its cross section resembles an equilateral triangle with smoothened apices.

The diploid chromosome number is $2n = 34$.

The bearded seal is the largest member of the 10-incisored seals (Phocinae). The body length of adults (seen as a whole) measured from tip of snout to end of tail along the dorsal curvature (L_c) is 195-255 cm and in a straight line (L_{cv}) 175-240 cm. The average length of animals from the Soviet western arctic along the body curvature (L_c) is 233.6 cm in males and 239.2 cm in females²²; the corresponding measurements in a straight line (L_{cv}) are 222.0 and 222.5 cm (V.A. Potelov). The average values for the Bering Sea bearded seals do not, however, reveal differences between males and females along the body curvature (L_c) (males 240 cm, females 239 cm) while in a straight line (L_{cv}) males are larger (225 cm) than females (217 cm) (Kosygin, 1966).²³ The axillary girth of adult bearded seals of the Barents and Kara seas averages 152.5 cm in males and 156.0 cm in females; these values for the Bering Sea animals are 161.0 and 148.8 cm respectively.

The condylobasal length of the skull of adults is 200-240 mm, average 220.5 mm,²⁴ width at mastoids 130-140 mm, and rostral width 40-50 mm.

The length of the os penis of adults varies from 10 to 15 cm.

The weight of the largest animals may reach 360 kg but the usual range is 225-320 kg. Males are roughly 25-35 kg heavier than females. The Bering Sea males average 277 kg, females 242 kg (Kosygin, 1966);

²² These sexwise differences (as also some others mentioned above) are difficult to explain biologically and evidently are the result of an inadequate number of measurements, especially of the males.

²³ The difference in average length in a straight line is evidently explained by the inadequate number of males measured by this method (four males versus 20 females).

²⁴ Data of Chapskii (1938), Potelov (1968*), and G.M. Kosygin.

the Barents Sea males weigh on average 256 kg, females 265.5 kg (V.A. Potelov). (K.Ch.)

Taxonomy

Only species of the genus.

Geographic Distribution

The basin of the North Atlantic Ocean, the arctic waters of the Atlantic from the Canadian archipelago to the Norwegian and Barents seas, and the northern and northeastern boreal-arctic zone of the Pacific Ocean (Bering Sea and the Sea of Okhotsk).

It is quite difficult to establish the northern limit of the distribution in the Arctic Ocean. Some wandering animals in summer stray very far from the coasts into the Central Polar Basin and are found among ice
138 floes in very deep waters. Particularly F. Nansen (north of 82° N lat.) and Ch. Sverdrup (around 85° N lat.) and Soviet explorers during their sojourn in the icebreaker "Georgii Sedov" in 1938 reported the recovery of a bearded seal. They also reported these records in the region of some drifting stations of "Severnyi Polyus". Some animals entered directly into the North Pole region where they were reported by R. Amundsen in 1925 and also by the Soviet polar explorers of "Severnyi Polyus-I" in 1937 and "Severnyi Polyus-3" in 1954, etc.

Geographic Range in the USSR

Constitutes roughly about one-half of the total range of the species, i.e., its Eurasian sector, and much of the Pacific Ocean region (Fig. 100).

The distribution is mainly the result of three natural factors: cold waters, presence of ice floes, and shallow depths. The bearded seal therefore descends to 60° N lat. or more southward only at places where these conditions are generated by cold currents, i.e., near the Labrador and southern Greenland coasts, in the Sea of Okhotsk, and the Tatar Strait. Being predominantly a benthic feeder and hence biologically associated with shallow depths, this seal usually does not stray beyond the continental shelf and prefers depths of up to 100 m.

Sightings of this seal in pelagic regions at great depths is more often the result of drifting ice floes. In some cases it is evidently caused by migrations also or is merely a random straying.

In the Barents Sea in the northwest along the Murman coasts, the distribution extends in a narrow belt to east of the boundary with Norway and enlarges along eastern Murman into the White Sea Inlet. Near

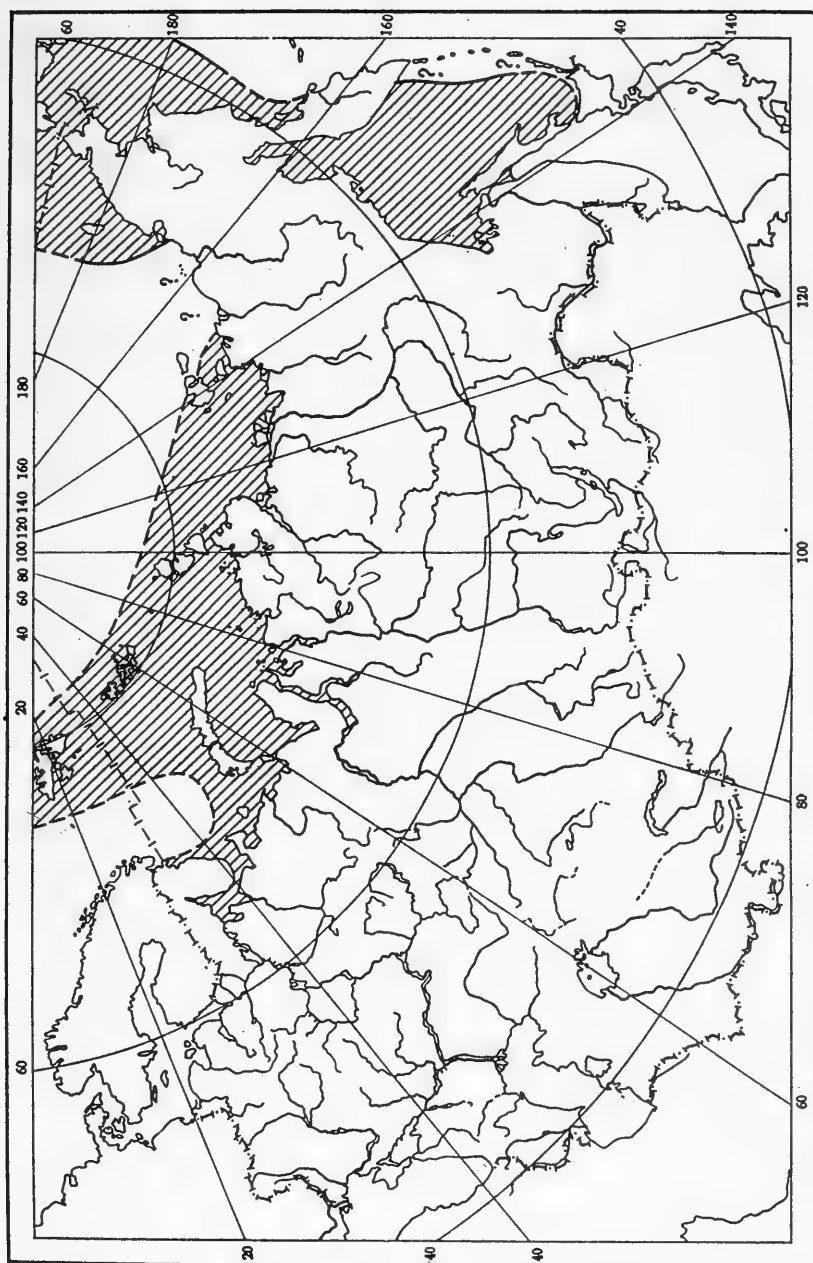


Fig. 100. Range of the bearded seal, *Erignathus barbatus* in the USSR (K.K. Chapskii). Broken line depicts the assumed boundary.

the meridian 40° E long., depending on the position of the ice rims, the boundary of distribution steeply turns northward; there, it encompasses not only the entire shallow water zone of the southeastern Barents Sea from Kanin Peninsula to the coasts of the Vaigach Peninsula and the southern part of Novaya Zemlya including Cheshsk Bay, Kanin-Kolguevsk shallow water zone and the Pechora Sea to Yugorsk Shar and Kara Strait, but also the pelagic regions. The latter include in particular the very broad Novaya Zemlya belt of the Barents Sea tending northwest, north, and northeast to the northern extremity of Novaya Zemlya. From there the distribution opens up like a fan toward the Kara Sea and also in the direction of the Franz Josef Land archipelago, including it. All other—central, northern, and western—generally pelagic regions of the Barents Sea are practically outside the limits of the range.

The bearded seal colonizes the White Sea almost everywhere but with different densities in different seasons and in different regions. Apparently it very rarely enters the extreme southern parts of the Onezhsk and Dvinsk bays (V.A. Potelov).

It is extensively distributed in the Kara Sea where it is quite common. In the western part of the sea it is found mainly in the shallow waters between the Vaigach and Yamal peninsulas, in Baidaratsk Bay, in the region of White Island, as also on the eastern banks of Novaya Zemlya and even in the pelagic zone of the western part of the sea south of Cape Zhelaniya, drifting there on ice floes. Farther east of White Island, the range covers the waters surrounding Shokal'sk Island, the northern part of the Gulf of Ob, and Yenisey Gulf.

In many regions where the habitational conditions for this species are less favorable (deficiency of food, continuous ice cover, extremely shallow depths, freshwater conditions, etc.), the boundary recedes slightly north of the continental coastline. Thus the bearded seal inhabiting the Gulf of Ob usually does not enter its southern part although its presence has been reported in the Ob' estuary (Brandt, 1856); it has not been sighted in the deep waters of Tazovsk and probably Gydayamsk bays. Evidently it does not go far south even in the Yenisey Gulf though it is encountered in its northern regions. It inhabits everywhere in the more open Pyasinsk Bay and even enters the Pyasina River (Heptner, 1936). It is encountered on the highly rugged western Taimyr coast, abounding
139 in islands, the Vil'kitsk Strait, and the coastal regions of southwestern Severnaya Zemlya.

How far north the range extends into the Kara Sea sector is not wholly clear but it has been reported time and again on the western coasts of Severnaya Zemlya. It has been encountered at the same latitudes and,

more westward, in the pelagic portions of the sea between Severnaya Zemlya and the Franz Josef Land archipelago.²⁵

Information on the distribution of the bearded seal in the Laptev Sea is still scant. It is encountered regularly in Vil'kitsk Strait, especially in the spring-summer period; its breeding grounds are known in the Cape Chelyuskin region (Tyulin, 1938; Rutilevskii, 1939). These animals reach the breeding grounds in large number from the Laptev Sea (Rutilevskii, 1939). They were noticed, albeit not frequently, on the coasts of eastern Taimyr (L.N. Popov, 1939), close to Begichev Island (Koshkin, 1937), and on Preobrazheniya Island (M.P. Vinogradov, 1949). They were reported on the Novosibirsk Islands (reports of the Russian Polar Expedition, 1900-1903).

The habitation of the bearded seal even farther eastward in the coastal waters of the eastern parts of the Laptev Sea and in the East Siberian Sea, reported in the last century, has been confirmed by other references also. One of them, though not very reliable, pertains to the Yana estuary (Bunge,* 1887) and another to the Kolyma estuary (Iokhel'son, 1898). Such limited information led, in turn, to the assumption of a fragmented range for this seal in the East Siberian Sea. Some latest observations reported from the eastern part of this sea, i.e., from the region of Chaunsk Bay, coastal areas east of Cape Shelag'sk, and areas directly adjoining Wrangel Island (Mineev, 1936; Fedoseev, 1966; and others), suggest that the Pacific bearded seal is found on the eastern fringe of the East Siberian Sea. On the other hand, we cannot ignore other reports indicating that in the more western parts of this sea, including the Kolyma region, the Pacific bearded seal is not only extremely rare, but is totally absent (V. Arsen'ev, 1935; Mikhel', 1938*; Rutilevskii, 1962). Evidently the Asian boundary between the ranges of the subspecies *E. b. barbatus* and *E. b. nauticus* traverses somewhere in this sea and not in the Laptev Sea, as stated by some (Scheffer, 1958; King, 1964).

The western part of the Chukchi Sea, including the Wrangel and Herald islands wholly fall in the range. The bulk of the population here is in the coastal belt between the Chukchi coast and the pack ice masses in the zone of drifting ice floes, as also in the immediate proximity of the coasts. These seals enter the much higher latitudes of the sea depending on ice

²⁵ Distribution of the bearded seal in the Kara Sea is based on the following sources: Nosilov (1911*), Zhitkov (1913, 1924), Heptner (1930), S. Naumov (1931), Kolyushev (1933, 1936*), Probatov (1933), Lepin (1936), Rundan (1936), Esipov (1937), Kirpichnikov (1937), Mikhel' (1937), Antipin (1936*), Rutilevskii (1939), Laktionov (1946), Tarasevich (1963), and others, as also V.L. Vagin, G. Galkin, L.I. Leonov, V.N. Nikitin, V.A. Potelov, A.N. Tyulin, K.K. Chapskii, I.K. Yakimovich, and others.

conditions and degree of ruggedness of the permafrost in the summer-autumn period (Leonov, 1953; Tikhomirov, 1966; Fedoseev, 1966; P.G. Nikulin, and others). It is not entirely clear whether the Chukchi Sea is one of the regions of their permanent habitation, i.e., whether these seals are found here in all seasons or mainly in summer. Although Pacific bearded seals have been reported northwest of Wrangel Island even on October 10, it is quite likely that most of them move into the Bering Sea in winter. There are, however, references leading to an opposite conclusion (Razumovskii, 1931*; V. Arsen'ev, 1935; Jonson *et al.*, 1966).

The Bering Strait region falls wholly in the range of the Pacific bearded seal. Its boundary diverges from here southward: in the west into the Gulf of Anadyr, in the southeast and south (roughly along the
140 meridian 175° W long.) toward the Pribilof Islands near which it turns east and northeast. The western branch of the Bering Sea portion of the range extends in a broad belt corresponding to the boundary of the maximum extent of the range to the south of drifting ice floes and to the west up to the coastal zone in the region of Cape Navarin (Tikhomirov, 1964, 1966; Kosygin, 1966). From here the range descends in a narrow border to the southwest along the Koryaksk coast to Olyutorsk Gulf and later slightly enlarging along the coastline, reaches Karagin Gulf. Farther south, on the eastern coast of Kamchatka, the range is actually interrupted although some authors have included all the Kamchatka waters in it (Freiman, 1936; Kurcheva, 1954*).

The Commander Islands also cannot be regarded as the zone of normal distribution of this species since the finds there are only rare (Barabash-Nikiforov, 1936) or extremely rare (Marakov, 1968). Similarly, this seal is rare on the Kuril Islands. It enters the region of the Commander Islands evidently from Karagin Island, most probably transported by broken ice floes which ultimately break up and thaw.

The Pacific bearded seal does not inhabit the whole of the Sea of Okhotsk. The range in this sea could be represented schematically in the form of an arc open toward the central portion of the Kuril range. Thus the southeastern part of the sea apparently falls outside the normal range. The boundary of the latter at this place describes a half loop extending from the southern Kuril Islands roughly along the meridian 155° E lat. to north-northeast and curves toward the midsouthern portion of the western coast of Kamchatka at some places on the latitude of Bol'sheretsk or even more northward. The rest of the areas in the Sea of Okhotsk, north, northwest, and northeast from this line (fluctuating to some extent depending on the position of drifting ice floes) to the coastline of the mainland and the coasts of Sakhalin, constitute the Okhotsk

part of the range of the Pacific bearded seal. It thus covers the Shelikhov Gulf, Penzhinsk, and Gizhiginsk bays up to their northernmost sections, the entire mainland zone to the north and northwest of the sea including the portion known as the Shantarsk Sea. Farther south the western region of the Okhotsk portion of the range extends in a broad belt from the Gulf of Sakhalin along the entire flank of Sakhalin, terminating in the southern portion of the sea between La Perouse Strait, Japanese waters (on Hokkaido Island), southern Kuril Islands, and the southeastern boundary of the range.²⁶

The Pacific bearded seal is practically absent in the Sea of Japan *per se* but for extremely rare episodic finds whose reliability is doubtful. In Tatar Strait, however, the boundary traverses evidently slightly south of the De Kastri latitude (S. Naumov and N. Smirnov, 1936).

A characteristic feature of the range of this species in the west (in the Barents Sea) and in the east (in the Bering Sea and the Sea of Okhotsk) and also to some extent in the expanse of the Siberian polar seas is its fairly well manifest seasonal variation due to the influence of ice cover dynamics and ice drift. The maximum boundaries of the range described above mostly pertain to the winter-spring season, while the real picture of the distribution of the animals in the other seasons is quite different. At places, for example in the Barents Sea, Bering Sea, and the Sea of Okhotsk, the range narrows toward the end of summer and in autumn and extends in a narrow belt into the coastal zone. On the other hand, in the Siberian arctic seas it is more extensive due to ice movements and thinning of ice floes in the summer (see "Seasonal Migration," pp. 196-198).

141 *Geographic Range outside the USSR (Fig. 101)*

In the European waters along the coasts of northern Norway, it extends from Varanger Fjord to North Cape and even down to Troms. In more severe winters the animals enter farther south up to Vesterålen, but invariably in small numbers. The bearded seal is common in Spitsbergen but encountered only sporadically along the northwestern coast of Iceland. Farther westward, the range covers the Greenland waters along the eastern coast from Cape Farewell to Datsk harbor of slightly more northward along the western coast up to Robson Strait; the eastern parts of the Canadian archipelago in Kane Basin, Baffin Bay, and Davis Strait;

²⁶ The review of the Okhotsk portion of the range has been compiled from the data of Ognev (1935), Freiman (1936), Nikulin (1937), S. Naumov (1941), Pikharev (1941, 1948), Kurcheva (1955), Tikhomirov (1961, 1966), Fedoseev (1970), Fedoseev, Gol'tsev, and Kosygin (1970), and some other sources.

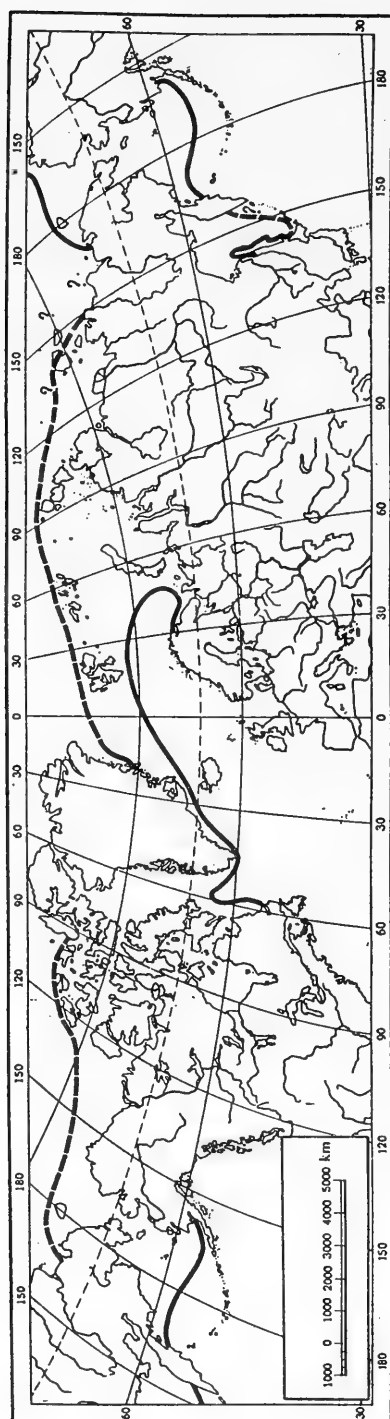


Fig. 101. Distribution of the bearded seal, *Erignathus barbatus* (K.K. Chapskii).

and the coastal zone of Labrador in the south to the eastern coast of Newfoundland (extremely rare here). The range in the west covers the entire periphery of Hudson Bay, Foxe Basin, Gulf of Boothia, Lancaster Strait, and the waters of Cornwallis Island. Still farther westward, along the southern mainland straits, the range reaches the Beaufort Sea and the Alaskan coasts where the range of the Atlantic bearded seal joins (?) with the extreme eastern branch of the range of the Pacific bearded seal. The range covers the entire coastal waters of Alaska from its northern coast to Bristol Bay including the region of St. Lawrence, St. Matthew, Nunivak, and Pribilof islands. South of the Sea of Okhotsk, it extends into the waters of Hokkaido Island. (K.Ch.)

Geographic Variation

In spite of recognizing two subspecies, Atlantic (*E. b. barbatus* Erxleben) and Pacific (*E. b. nauticus* Pallas) quite long ago (Miller, 1923; Ognev, 1935; N. Smirnov, 1935; S. Naumov and N. Smirnov, 1936; Vinogradov, 1949; Ellerman and Morrison-Scott, 1951; Scheffer, 1958; Chapskii, 1963; and others), no one has conclusively defined their morphological characteristics. "The distinctive features of *E. b. nauticus* are generally not quite distinct as they overlap each other, and many of them can be recognized only when comparing in a large series" (S. Naumov and N. Smirnov, 1936). This situation is relevant even today.

1. Atlantic bearded seal, *E. b. barbatus* Erxleben, 1777 (syns. *leporinus*, *parsonsi*, *lepechini*).

The body dimensions and weight are slightly less; the skull in most of the animals has very narrow and long nasal bones, imparting a very elegant appearance.

The body length measured in a straight line (*L_{cv}*) averages 220 cm and the axillary girth 152.5 cm. The condylobasal length of the skull averages 220-221 mm and the zygomatic width 130 mm. The length of the nasal bones averages 21.5 mm and width 6.5% of the condylobasal length.

Ecologically, this subspecies exhibits a distinct pagophile tendency. The western part of its range covers the White, Barents, Kara, and Laptev seas.

Outside the USSR, the range covers northern Norway, Spitsbergen, Greenland, and the Atlantic portion of the Canadian archipelago.

2. Pacific bearded seal, *E. b. nauticus* Pallas, 1811 (syns. *albigena*, *laktak*).

Slightly larger than the Atlantic subspecies. The color is quite monochromatic, often with a rust tinge in the cervical zone. The nasal

bones in most animals of this subspecies are broad in the anterior part and narrow very sharply toward the apex.

The body length in a straight line (*L_{cv}*) averages 227.5 cm and the axillary girth 161 cm. The condylobasal length of the skull averages 225.5 mm; length of nasal bones 17.5% (average) and width 8.1% of the condylobasal length.

Ecologically, this subspecies tends notably toward coastal land where it forms rookeries.

The eastern part of the range in the USSR covers the western regions of the Chukchi Sea and evidently the easternmost regions of the East Siberian Sea as also the Bering Sea and the Sea of Okhotsk.

Outside the USSR, the range covers the Bering Sea portion of Alaska, northern Bristol Bay, and the Alaskan side of the Chukchi Sea up to the western extremity of the Beaufort Sea (Chapskii, 1963). The differences between the Atlantic and Pacific forms were later confirmed (Kosygin, 1969) but doubts arose once again (Kosygin and Potelov, 1971*). (K.Ch.)

According to the most recent data (Chapskii, in litt.), these subspecies are entirely valid.

Biology

Population. No accurate census of the bearded seal is available to date either within our waters or in the other regions of its range. In the 1950s, the total world population was approximately put at 75,000-150,000 (Scheffer, 1958; King, 1964).

In the 1960s, an attempt was made to approximate the total population in the arctic and subarctic seas surrounding Eurasia. Various indirect data, including the probable eastern Canadian population put at 200,000 (McLaren, 1958), were used for this purpose. The resultant highly approximate figure of 400,000 (Chapskii, 1966) reflects more the probable maximum and surpasses the actual numbers, which no doubt do not exceed 300,000 at the most.

The distribution of this population is uneven. Its presence in large numbers is confined to the following major sections of the range: (1) southeastern part of the Barents Sea, (2) southwestern part of the Kara Sea, (3) eastern extremity of the Kara Sea, (4) Sea of Okhotsk, and (5) northern and northeastern regions of the Bering Sea. Each of these regions holds a substantial concentration of the animal in different seasons. It is probable that the maximum possible potential for the population growth prevails in the Barents-Kara region although the Sea of Okhotsk has been holding first position in terms of catch in recent years.

The Bering Sea reserves are less than those in either of the first two regions individually.

In the western arctic USSR and in the White Sea the maximum concentration of the bearded seal (sighting or catching over 100 animals per day of hunting or ship survey) was noticed in the following regions: (a) northeastern part of the White Sea Inlet and the southern part of the Barents Sea adjoining the northern extremity of Kanin Peninsula; (b) sections of the Barents Sea between the Kanin and Kolguev peninsulas, western part of Cheshsk Bay; (c) eastern belt of the Barents Sea near Novaya Zemlya (close to the southwestern coast of southern Novaya Zemlya Island; the section of the sea opposite Matochkin Shar Strait; and zones of Admiralty Peninsula and Cape Zhelaniya); (d) Franz Josef Land archipelago; and finally (e) the easternmost corner of the Pechora Sea, near Yugorsk Shar.

The regions with a somewhat smaller population (50 to 100 animals sighted per day) are: Kandalakshsk and Mezensk bays, other sections (apart from those mentioned) of the Kanin-Kolguev shallow waters (at Barmin Headland and north of Kolguev Island) and the Pechora Sea (at



Fig. 102. A female bearded seal emerging from water. Barents Sea, April, 1967 (photograph by V.A. Potelov).

Russk Bend and Kara Strait). In the western part of the Kara Sea the regions that are as abundant are primarily Yugorsk Shar, Baidaratsk Bay, north of White Island, and then the Kara Strait zone and on Matochkin Shar. In the eastern part of the sea bearded seals in largest numbers are noticed north of Pyasinsk Bay, in the region of the Minin reefs and more toward the open sea (slightly east of the arctic archipelago islands), and also almost in the eastern extremity of the sea, slightly west of Severnaya Zemlya (west of Shokal'sk Strait). The bearded seal is seen in smaller but yet significant numbers north of Dixon Island, in the region of Nordenshel'd archipelago, and also right in Shokal'sk Strait and on Pioneer Island (V.A. Potelov).

The disposition of the bearded seal has, however, undergone some definite seasonal dynamics (see p. 187).

In the Sea of Okhotsk the bulk of these seals is concentrated in the spring in the northeastern extremities of the sea, in the lower sections of Shelikhov Gulf, including Yamsk Bay, around Zabiya, Babushkin, and other straits in the northern strip of the sea in the west to Ushka Bay; it is also seen not far from the northwestern coasts of Kamchatka (Freiman, 1936; Pikharev, 1948; Tikhomirov, 1961). In the northern part of the sea the vast majority of the Pacific bearded seals is confined in the spring-summer period to the "inner" edge of drifting ice floes turned northward (toward the coast) (Fedoseev, 1966). Among the regions with abundant Pacific bearded seals until comparatively recently were the western part of the sea near Sakhalin, mainly Terpeniya Bay and, in a slightly later season, the Gulf of Sakhalin and the region of Shantarsk Islands with the adjoining Academy, Nikolai, Ul'bansk, Tugursk bays, etc. (S.P. Naumov, 1941; and others).

In the Gulf of Sakhalin and farther west of Cape Litke in the direction of Shantarsk Islands, hunters daily counted a few hundred Pacific bearded seals at the beginning of the season (Pikharev, 1948). This situation is no longer true.

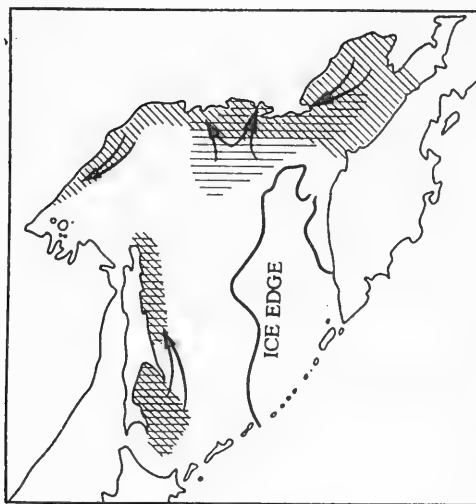
In the mid-1960s, some attempts were made to count the Pacific bearded seal on the spring-summer ice floes of the Sea of Okhotsk (Tikhomirov, 1968). The areas of some nurseries and molting colonies did not generally exceed 50-100 km² and the total population was determined in such colonies (500-1,000 animals maximally). However, the precise number of such "spots" was difficult to count and hence it was impossible to arrive at a grand total for the population. The Sea of Okhotsk stands fourth in the relative population of the Pacific bearded seal, after the ringed seal, ribbon seal, and evidently the larga.

It is quite likely that two local populations of the Pacific bearded seal exist in the Sea of Okhotsk. One of them is in the northern part

of the sea tending mainly toward the expanses from Lisyansk Peninsula to Tauisk Bay and farther to Babushkin, Kekurnyi bays, and Shelikhov Gulf. Another population inhabits the southwestern part of the sea, including the entire region close to the eastern coast of Sakhalin Island, the Gulf of Sakhalin and the region of Shantarsk Islands (Fig. 103). In the pupping season this "Sakhalin" Pacific bearded seal is concentrated in Terpeniya Bay and in the air holes and open pools on the eastern coast of the island. With the breaking up of the ice floes in spring, the Pacific bearded seal migrates to the Gulf of Sakhalin and the Shantarsk Islands.

The population density of the Pacific bearded seal in the breeding colonies estimated by aerovisual surveys in 1967-1969 did not exceed on average 0.2-0.8 per sq. km.

145 There are no geographic isolations between the populations of the Okhotsk Pacific bearded seal and they freely intermix. It is therefore quite possible that in summer, when these seals are widely dispersed along the shelf zone of the Sea of Okhotsk, their populations could partly intermix. The 55-56° N lat. could be regarded as the tentative boundary between the northern and Sakhalin populations of the Okhotsk Pacific bearded seal.



144 Fig. 103. Main regions of concentration of the Pacific bearded seal, *Erignathus barbatus nauticus*, in the Sea of Okhotsk at the time of whelping and the migratory course of its population for molting (G.A. Fedoseev).

The number of Pacific bearded seals in the Sakhalin population by aerovisual surveys was put at 35,000 - 40,000 and the population in northern Okhotsk at 145,000 - 160,000 (Fedoseev, 1970; Fedoseev, Gol'tsev, and Kosygin, 1970*; G.A. Fedoseev).

In spring and early summer the bulk of these seals concentrate in the central region of the northernmost part of the Bering Sea, in a belt close to the edges of drifting ice extending between the St. Lawrence and St. Matthew islands. The population here is only slightly less than that of the other two proximate colonies in the strip of drifting ice floes continuing in a southeastern direction: one directly to the southeast of St. Matthew Island and the other even farther toward the Pribilof Islands and Bristol Bay roughly at the meridian of Nunivak Island. The disposition of these groups depends on the actual ice conditions in a given year.

One more fairly distinct population is grouped on the ice floes in the western part of the Gulf of Anadyr²⁷. In the relative population of seals during the icy period in the pelagic portions of the Bering Sea, the Pacific bearded seal once again holds last place at 10-12% of the total population (Tikhomirov, 1964; Kosygin, 1966). The factual relative proportion of this species is even less since the calculations did not take into consideration the ringed seal, as it is generally extremely rare in the pelagic regions of the sea.

The total population in the Bering Sea section of the range is less than the corresponding numbers in the Sea of Okhotsk. The population is even less in our section of the Chukchi Sea. It is not clear whether or not the populations of the Bering and Chukchi seas are totally isolated since there is information that the Pacific bearded seal wanders from one sea to the other (see p. 198). The populations in the Laptev Sea and in the westernmost part of the East Siberian Sea are most dispersed. East of the Siberian Sea, the population rises quite rapidly and in the Chaunsk Bay region and more eastward, the Pacific bearded seal becomes quite common though less numerous.

Habitat. The habitat varies in different parts of the range and in different seasons. Regions with a high rugged coastline with bays and islands which offer protection from storms and from the piling up of ice floes are the most favorable. The bearded seal avoids very shallow open coasts since they do not provide adequate food ("plowed" by ice) and are exposed to coastal waves and are generally less favorable for habitation

²⁷ Distribution of the most important concentrations of the Pacific bearded seal in the Bering Sea is based on the observations of Tikhomirov (1964, 1966b), Kosygin (1966a, b), and K.K. Chapskii.

of such a large animal. Its typical habitats are not in the continental shelf but the shallow waters (a few tens of meters deep) where it is confined because it essentially survives on benthic food. This is the primary reason for the predominant distribution of the population in such shallow waters as found in the Kanin-Kolguev, Baidaratsk-Yamal'sk bays, and the Gulf of Anadyr, northeastern regions of the Bering Sea shelf, and the shallow-water periphery of the Sea of Okhotsk.

146 The increasingly freshwater sections of the straits and bays in the mouth zones toward the western (Atlantic) part of the range hold little attraction for this seal; its transgression even into the major rivers is a rare phenomenon. These animals are found rather infrequently even in the mouth and estuarine zones. The affinity of the Far-Eastern Pacific bearded seal for rivers is altogether different. It readily takes to some rivers in the Sea of Okhotsk, Amur lowland, and also not infrequently in the Gulf of Anadyr. The factors responsible for these transgressions are not fully understood. It is possible that sometimes, under conditions of exposed coasts (as on the western coast of Kamchatka), this is the result of seeking sites well protected from storms and possibly the massive availability of some common tiny fish. In the western part of the Sea of Okhotsk the Pacific bearded seal is regularly found in the summer-autumn period in shallow bays, such as Ul'bansk, Nikolai, and Konstantin. Here, during low tide shoals and banks are exposed over much of the river mouth zone which these animals use readily. The reason for their affinity for such zones is apparent from the example of the formation of rookeries in the upper courses of Ul'bansk Bay in the fore-estuary areas which dry up in low tide. The animals initially enter the river (Syran) and later crawl onto the dried-up laidas [low coastal plains dissected by tortuous rills]. In the immediate proximity of the sea, the animals do not crawl onto the laidas probably because of the unusually high viscosity of the bottom and the extremely significant shallowness in the adjoining sections of the sea. The bulk of the animals take advantage of the fairway (S. Naumov, 1941).

Something similar is noticed along the coasts of western Kamchatka too. "In summer the Pacific bearded seals are encountered in the shallow-water bays with abundant reserves of bivalves and tiny crustaceans and sometimes ascend with the high tide into the river. . . . At the end of October, more Pacific bearded seals than larga or ringed seals begin to appear in the summer. . . . At this time, during low tides at night the Pacific bearded seals love to rest on the dried-up river banks or the laidas in the estuary" (Lun', 1936).

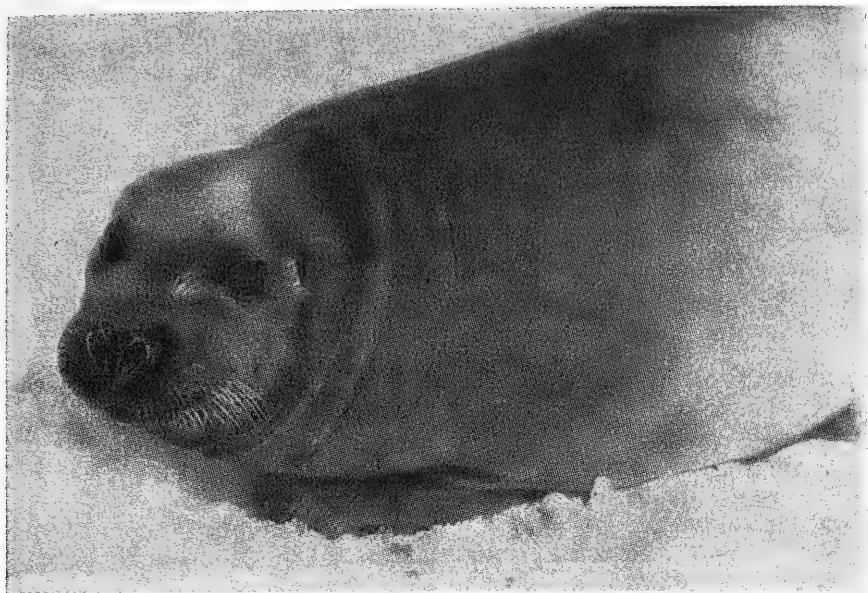
The rookeries are formed on low pebbly banks or sandy shoals and also on banks consisting of pebbles, quite often with an admixture of

significant quantities of silt and some small boulders. Only rarely, stray animals or small groups are seen on smooth rocks or rocky platforms. In Konstantin Bay the substrate under the rookeries on the drying-up banks is extremely shallow on one side and very deep on the other; the animals are seen on the deep side.

The coastal rookeries of the Okhotsk Pacific bearded seal are formed during low tide and are occupied from the second half of summer and autumn until the appearance of ice floes on the coasts. From this time, the concentration of animals decreases and they begin to stray from the coasts and are seen singly on ice floes. Depending on the ice conditions on the coasts, they go out deeper into the sea and remain among drifting ice floes. In the strip of fixed shore ice, locking up the coast with a continuous cover, this seal is encountered only on the edges where there are open waters and mobile broken ice floes. For respiration and emerging onto ice whenever possible, it uses the natural openings in the ice floes, such as open pools, air holes, and crevices. Liberally using its claws, it resorts to making air holes and the like only in extreme cases, though it is capable of making them as well as the ringed seal (N. Smirnov, 1927). Most recent investigators regard the bearded seal as an inhabitant of only drifting ice floes interspersed with open water pools. In this context even its ability to make and regularly maintain air holes in the ice has generally been doubted although some rare exceptions are possible (McLaren, 1958; Mansfield, 1963; and others). In the spring-summer period, it is confined to drifting ice floes and when some food is available, it can be found even at considerable depths.

The bearded seal exhibits not much choice of floes in the spring-summer period but nevertheless prefers low ice floes that have not become hummocky (Fig. 104). These may be very extensive or very small and hardly capable of supporting the animal. It rests mainly on pure white ice, avoiding "soiled" ice floes and uses the latter only in extreme cases when there is no alternative. Quite often, it rests on very thin and
 147 weak ice floes and appears from a distance to be lying directly on the water (Pikharev, 1941). In most cases it selects the edges of drifting ice floes but at some distance from the very edge, free from surges. It is also found far from the edge and clearly avoids large, highly compacted edges of ice floes. It rests singly, often in pairs, and in threes at the very edge of an ice floe.

Food. The bearded seal gets at food predominantly from the bottom or close to it, mainly from depths of up to 50-60 m. The limits of its submergence have not been established but evidently 100 m is not the limit.



147 Fig. 104. Pacific bearded seal on an ice floe. Bering Sea (photograph by G.M. Kosygin).

The animal food consumed by this seal is diverse but the preferential or more accessible species are readily distinguished. In this respect, much depends on the local features of the deep-sea fauna as also to some extent on the time of year. In general, over 70 species of invertebrates and fish have been identified in the diet of this seal. However, in a given region and season, a relatively small number of species serve as the basic food. Most often, crustaceans, mollusks, worms, and echiurids are found in the food; it also consumes large amounts of fish, especially the polar cod. Crabs and shrimps predominate among the crustaceans; amphipods and isopods are consumed far more rarely. Mollusks are represented by some massive species of gastropods, mainly of the genus *Buccinum*, more rarely bivalves. Cephalopoda are seen in its food relatively rarely. From among the worms, the various members of Polychaeta—*Pectinaria*, *Arenicola*, *Harmathoe*, etc. are consumed. Echiurids (mainly *Echiurus echiurus*) play a noticeable role in its food while *Priapulus caudatus* has a subordinate role. Sponges, sea cucumbers, even sea anemones, and others, broods of mollusks, and sometimes fish spawn have been found time and again in the stomach of this seal.

The food composition of the White Sea bearded seal is as follows: fish about 30% (of the total number of stomachs examined), crustaceans 77%, gastropods 10%, bivalves 5%, worms 2.5%, and others 2.5%. The

composition of the fish is quite diverse with the polar cod holding first place, followed by plaice (*Pleuronectes platessa*), common sand eel (*Ammodytes hexapterus*), herring (*Clupea harengus*), and more rarely
 148 navaga (*Eleginus navaga*), cod, haddock (*Gadidae*), and sometimes even sea trout (*Salmo trutta*) and nelma (*Stenodus leucichthys nelma*). The last two species are consumed very rarely when the seal transgresses into a river, as for example the Shoina. Crustaceans are represented almost exclusively by decapods, mainly crab (*Hyas araneus*), rarely shrimps (*Sclerocrangon boreas*, *Eualus gaimardi*, *Hetairus polaris*), and sometimes amphipods (*Anonyx migax*). Gastropoda are represented exclusively by the genus *Buccinum* and bivalves by *Cardium ciliatum*. From among the rest of the groups, *Priapulius caudatus*, *Cucumaria frondosa*, and ascidians are found rather rarely (V.A. Potelov).

The specific proportions of the most important components in the food of the Barents Sea seals are as follows: fish 65%, crustaceans (decapods) 67.5%, amphipods 12.5%, gastropods about 20%, bivalves 8.5%, cephalopods 4%, worms 14%, sea cucumbers 4%, and others 7%. The fish food is even more diverse than in the White Sea. Apart from the polar cod, flounder, and herring (consumed at places in large quantities), as also navaga, sand eel, and cod with haddock (consumed rarely), the bearded seal quite often feeds on goby (*Cottus tricuspis*) and sometimes also blennies (*Lumpenus* sp.), and skate (*Raja* sp.) (V.A. Potelov); according to earlier data (Wolleback, 1907), capelin and sea bass are consumed from time to time.

From among the crustaceans, this seal consumes more often crabs (*Hyas*) and shrimps (*Sabinea*), more rarely *Sclerocrangon ferox*, *S. boreas*, and also sea slater (*Mesidothea entomon*) (V.A. Potelov). It also consumes *Eualis gaimardi*, *Eupagurus pubescens*, *Spirontocaris palaris*, Hippolytidae, and sometimes many species of amphipods: *Anonyx nugax*, *Stegocephalopsis ampulla*, *Acanthonoroma* sp., *Gammarus locusta*, and *G. homari* (Chapskii, 1938).

From among gastropods, species of *Buccinum* hold first place, sometimes supplemented by species of the genera *Natica*, *Septunea*, and *Acrybia flava* (Chapskii, 1938). The bivalve most often found in the stomach is *Cardium graenlandicum*; also seen are mollusks, such as *Macoma calcaria*, *Astarte* sp., and species of the genus *Mya*, and *Saxicava arctica*, which are not characteristic of the food of the bearded seal (N. Smirnov, 1903, 1908). Sometimes it also consumes cephalopods, especially cuttlefish and squids (genera *Rossia*, *Ommatostrephes*) (Kondakov, 1932*; V.A. Potelov). It often consumes echiurids—*Echiurus echiurus* and polychaetes—*Arenicola* and *Harmathoe*, and from among the other

groups of benthos, the sea cucumbers *Cucumaria frondosa*, *Psolus*, and sometimes sea anemones, jelly fish, ascidians, and sponges.

Some local food characteristics have been noticed although they reveal no systematic pattern (because of paucity of data). Thus, in the Kanin-Kolguev shallow waters and in the Pechora Sea where the benthos abounds in the crab *Hyas araneus*, it forms an extremely significant proportion of the food of the bearded seal. Moreover, other crustaceans, mainly tiny shrimps (*Sclerocrangon boreas*, *Hippolyte* sp., *Sabinea septemcarinata*), and sometimes the sea slater (*Mesidothea entomon*) account for a large proportion of the food.

Crustaceans also play a predominant role in the food of the bearded seal on the western coasts of Novaya Zemlya (shrimps, but sometimes even amphipods). In its autumn-winter food, however, the polar cod almost takes first place.

In the Franz Josef Land archipelago, in the summer season, the bearded seal feeds mainly on gastropods while amphipods play a subordinate role.

In the Kara Sea the food composition reveals no perceptible changes. The percentage content of fish and amphipods is the same as in the case of Barents Sea seals; the indices for gastropods are quite close although the total proportion of mollusks is higher due to the greater intake of bivalves; the role of crustaceans here is low. The fish food of bearded seals in the Kara Sea is far less diverse. It consists almost exclusively of polar cod with an extremely small proportion of sand eel, and evidently sporadic arctic char and omul (cisco). The most important, frequently consumed crustaceans are crab (*Hyas araneus*) and shrimp
 149 (*Sclerocrangon* and some others); sea slater²⁸, and amphipods are secondary. Mollusks are almost invariably represented by gastropods (*Buccinum*, more rarely *Natica* and *Neptunea*), and in rare cases by scallops (*Pecten*). Cephalopods are regarded as of lesser significance while worms play a slightly greater role: polychaetes (*Chione*) and echiurids (*Priapulius bicaudatus*, *Echiurus echiurus*); sea cucumbers and ascidians from among the other groups are found rather rarely (V.A. Potelov).

Sometimes the animals are satiated with extremely diverse foods: only mollusks or exclusively shrimps (*Sclerocrangon boreas* and *S. ferox*) and sometimes isopods (*Mesidothea sibirica*, *M. sabini*) or fish alone. The diet is mostly mixed.

²⁸ Often found in the stomach of the bearded seal caught in the region of White Island (Tarasevich, 1963) although, according to V.A. Potelov, the sea slater represents more an obligatory than a favorite food.

In the western part of the Sea of Okhotsk the main food items in the spring are crabs (*Hyas coarctata*), echiurids (*Echiurus echiurus*), shrimps (*Sclerocrangon boreas*, *S. salebroso*, *Pandalus hipsinotus*), cephalopods, gastropods (mainly *Buccinum*) and bivalves, sea cucumber, and often sponges too, though the nutritive value of the latter is extremely doubtful. The full list of the food items of the Okhotsk bearded seal runs into several tens of species. In the deepest water region (northern Sakhalin) where the minimum depth is about 140 m, the food is less diverse: mainly shrimps (Pandalidae, Crangonidae), gastropods (*Buccinum*, *Chrysodomus*) and cephalopods (*Octopus* sp.), fish (smelt), and some others. Deep-sea animals, such as crabs, lamellibranchs, polychaetes, echiurids, sea cucumber, and others are also typical. At other places, these represent the most important food items of the Pacific bearded seal but here they play a minor role or are totally outside the diet of the seal.

In the northwestern extremity of the Gulf of Sakhalin where the depth is considerably less, the food of the Pacific bearded seal is more diverse but consists mainly of benthic components, the most important among which are the crabs (*Hyas coarctata*), echiurids (*Echiurus echiurus*), shrimps (Crangonidae, Pandalidae), as also gastropods and bivalves (Pikharev, 1941). The Shantarsk archipelago bearded seal exhibits a fairly "similar diet" with the exception of echiurids and gastropods, which are totally absent; the importance of bivalves, especially *Mya*, is sharply reduced (Pikharev, 1941; S. Naumov, 1941). In Tatar Strait, in May, the Pacific bearded seal consumes mainly shrimps (*Sclerocrangon*) and more rarely amphipods (Gammaridae) (Yu.A. Salmin).

In the Bering Sea the Pacific bearded seal feeds in the spring-summer period mainly on crustaceans, mostly snow crabs (*Chionecetes opilio*), shrimps, mainly *Crangon dalii* and *Nectocrangon lar lar*, and also species of the genus *Pandalus*; it relies to a lesser extent on other genera, such as *Sclerocrangon* and *Eualus*; the remaining groups of crustaceans, including gammarids and mysids form a small proportion of the food. Gastropods, mainly of the genus *Polynices* and others which were not identified fully, represent another group of preferred foods. Cephalopods (not identified to the generic level) can be placed in the third group of importance. Among the remaining invertebrates, worms constitute a noticeable proportion: polychaetes, as also *Priapulius caudatus*, *Echiurus echiurus*, and others (Kosygin, 1966, 1971*). Until recently, sand eel and daubed shanny (*Leptoclinus maculatus*) almost exclusively represented the fish constituents of the food; flounder (*Pleuronectes*) was very rarely found (Kosygin, 1966). It is now known (Kosygin, 1971*) that fish occupies an important place in the food of the Bering Sea bearded seal. The

150 stomach of 565 animals revealed 13 species of predominantly deep-sea fish: sand eel, daubed shanny, rattail, eelpout, leatherfin lumpsucker, two different genera of flounder, delta smelt, capelin, saffron cod (navaga), some type of bass, pricklyback, and pollock. Although these fish finds were noticed only in 9% of the animals inspected, the stomach of some seals actually contained some of them in quantities exceeding a hundred (capelin, daubed shanny, and sand eel).

No direct observations have been reported about the manner in which the seal obtains its food. However, from the intense wearing of the claws of the fore flippers in some animals, the rather frequent presence of sand and pebbles in the stomach, and also the presence of pits in the dried-up coastal belt, which, according to some researchers, were dug by the bearded seal (S. Naumov, 1941), it is assumed that the animal digs food out of the bottom (Pikharev, 1941). The seal has to dig the bottom to reach buried bivalves and worms. It is highly possible that this is done with the fore flippers as they have powerful claws.

Nevertheless, the bearded seal seldom has to dig for its food as most of its dietary items are not buried in the bottom (crabs, shrimps, amphipods, and other crustaceans and gastropods). Insofar as food animals such as *Priapulus caudatus*, which are not deeply submerged in the soft bottom are concerned, the seal senses them with its whiskers and can evidently easily get at them without using its flippers. The possibility of seizing some objects submerged in the soil directly by the mouth is suggested by the repeated finds of broken siphons of some bivalves in the stomach of these animals.

Assessments of the seasonal variations in the food of this seal are somewhat contradictory. From April to June, the stomachs of most of the Okhotsk bearded seals examined were empty. The conclusion was therefore drawn that this seal ceases to feed in spring (S. Naumov, 1941). According to other data, however (Pikharev, 1948), it continues to feed in spring but less intensively. The data obtained for the Bering Sea bearded seal (Kosygin, 1966, 1971*) point to some reduced intake in the summer season. A nearly similar picture emerges for the bearded seals of our western seas (V.A. Potelov).

Home range. This could not be ascertained with certitude although it can be suggested that different populations which undergo seasonal dynamics are confined to their own home ranges, as in the case of many other species. The solitary life of the animals of this species for much of the year is well known, but this characteristic varies depending not only on the season, but also the geographic region. In general, however, the western populations lead a more "cloistered" life while the Pacific

Ocean animals (in the Sea of Okhotsk) tend to form herds and beach rookeries in the latter half of summer and in autumn.

Hideouts and shelters. The construction of hideouts and shelters is not a general characteristic of this species. In the more severe arctic regions, for example in the Kara Sea, the bearded seals probably make snow holes or shelters, using for this purpose primarily the hollows in the snow hummocks that form near their air holes in an ice floe. Such snow holes were found far from the coast of Siberia (N. Smirnov, 1927) and around Cape Chelyuskin (Rutilevskii, 1939; A.N. Tyulin). The bearded seal was regarded as an inhabitant of these shelters based solely on the size of the hole and the dimensions of the lair, as these exceeded those of the ringed seal. These criteria are not reliable, however. Such shelters were not detected in other sections of the range.

The ability of the bearded seal to make pits in the ice has been
 151 known from at least the 1920s (N. Smirnov, 1927). The animals usually survive without them however, preferring zones of drifting broken ice floes. When the open water pools are covered with thin fresh ice, these seals, like others associated with ice floes, break the crust and keep the opening from refreezing by frequent use. Several such holes have been found close together, for example in the Sea of Okhotsk (Fedoseev, 1971).

In the northern European part of the USSR the bearded seal usually does not overwinter in the coastal belt which is permanently ice-bound ("fast ice"). But some young animals stray. Instances of such strays have been seen on the southern coasts of Novaya Zemlya. The young remained scattered in the winter in bays and straits covered with fast ice and were compelled, like the ringed seal, to make air holes. Cases of young bearded seals emerging from such holes onto thick spring ice have been noted in Rusanov Bay as well as in Petukhovsk Shar Strait (V.A. Potelov).

Daily activity and behavior. Prolonged observations of the same animals in nature are almost impossible. Nevertheless, it can be said with certainty that the activity of the animal does not weaken, but increases with the onset of twilight. Such nocturnal activity is confirmed by the numerous catches of the animals in fixed nets at night, particularly in autumn when they are trapped more often. In summer the animals prefer to warm themselves in the sun, resting on the ice.

At the end of March and early April 1967, in the northern part of the White Sea and in the southern part of the Barents Sea, bearded seals were found in the water until 8:00 a.m.; thereafter, until 12:00 noon, the number of animals in the water and resting on the ice was nearly equal. In the late afternoon hours, about one-fifth of the animals were in the water; from 4:00 to 8:00 p.m. the number of animals in the

water rose again to one-third (observations beyond this hour could not be continued because of darkness). Similar observations at August end in the Kara Sea also revealed maximum animal activity in the morning hours. Until midday, not a single animal was found on the ice while six were noticed in the water from 4:00 to 9:00 a.m. and 32 from 8:00 to 12:00 noon. In the course of two four-hour surveys in the afternoon, five animals were found in the water on each occasion and 10 and 54 on the ice. From 8:00 p.m. to midnight and in the first four hours of the following day, 26 animals were noticed in the water on each occasion and 24 and 12 animals on the ice.

In Baidaratsk Bay, from July 5 through 12, 1961, some 140 bearded seals were sighted from a hunting ship. The number of animals resting on the ice at different times of the day was (as % of the total number of animals counted in the corresponding intervals, averages): 8:00 a.m. to 12:00 noon—6%, 12:00 to 4:00 p.m.—31%, 4:00 to 8:00 p.m.—33%, 8:00 to 12:00 midnight—26%, and 12:00 to 4:00 a.m.—3%.

Thus in the morning hours almost all the animals remain in the water looking for food while their activity decreases throughout the day. Emergence onto the ice occurs exclusively in the second half of the day. From May end through July inclusive, they rest on ice for a considerably longer time than in other months (V.A. Potelov). A similar pattern was observed in the Sea of Okhotsk also. The Pacific bearded seals there are seen on the ice and in the water in spring and early summer at different times of the day. They crawl onto ice in the largest numbers after 10:00 a.m., especially in good weather on clear sunny days. At first they are quite restless but then fall asleep, sometimes very soundly. An animal resting on the ice can often be approached within 3 to 5 m without awaking it. The Pacific bearded seals sleep most soundly in good sunny weather (S. Naumov, 1941).

This seal is most often found singly on the ice, rarely in pairs or trios on a single floe, and extremely rarely in a group of five to seven animals; when in such a group, the animals remain apart, invariably along the very edge. The seal sleeps mainly on its side or on its back. In spite of its heaviness, the animal clambers quite easily onto ice. First, it thrusts its head high above the water for a survey, surfaces right up to the ice and, holding onto it with the fore flippers, heaves itself upward with a
 152 massive thrust of the hind flippers (Pikharev, 1941a*) or throws itself up in one leap. While diving, it usually reveals a part of its back and sometimes (evidently when at peace) the entire back and even the hind flippers.

In the period of formation of the beach rookeries in the Far East, activity is related not so much to changes in light and darkness as to ebb

and tide pattern, since the rookeries are formed on the receding water front and begin to break up with high tide. Our western hunters regard the bearded seal as an extremely timid animal while eastern hunters subscribe to the opposite view. Both are evidently right since the prolonged and intense killing of the animal in the Soviet western arctic seas has led to greater fright and caution than in the Far East. It is possible that even the name "sea hare," given to it by Russian hunters in the west, reflects to some extent the timid behavior of the animal.²⁹ In the water, however, it is bolder and permits the approach of man far closer than when on ice.

Seasonal migrations and transgressions. Ordinarily, these seals are regarded as settlers not given to en masse or prolonged migrations (N. Smirnov, 1908, 1929; Ognev, 1935; Freiman, 1936; S. Naumov, 1941; partly Tikhomirov, 1961; Shustov, 1964*; and others). In fact, the bearded seal does not perform migrations of the type characteristic of the Greenland [harp] seal. Nonetheless, the bearded seal cannot be regarded as a completely settled animal since its population almost everywhere undergoes fairly perceptible seasonal changes, largely due to changes in ice conditions and also probably depending on the distribution of food and selection of a site for reproduction, molt, and for setting up beach rookeries.

In the simplest case, the seasonal changes occur as follows: from the second half of summer and in autumn, the bulk of the animals is distributed in the coastal belt or in the shallow waters in the relatively warm sections of the range where ice floes have thawed. With the onset of winter and formation of the coastal ice cover, the animals usually leave the shores. Throughout the winter-spring period, they remain beyond the stationary coastal ice floes (fast ice) among drifting floes. In the eastern part of the Barents Sea many animals are found far away from the coasts, almost on the outer edge of the ice floes. As soon as the coast is free from fast ice, part of the population is distributed along it and settles preferentially in regions with a more rugged coastline, while the other part moves away with the ice floes. From the second half of summer, a reverse movement occurs: that part of the population which left the coast with the ice floes now returns.

Such a simple pattern of seasonal migrations is characteristic in many sections of the Sea of Okhotsk. At the beginning of winter, with the appearance of stable ice floes and depending on their spread, the Pacific bearded seal withdraws from the coasts to the outer edge of the coastal

²⁹ Others suggest that it was so named because it "hops" while negotiating on ice (or on land).

ice belt into the open water pools among mobile broken ice floes, moving with them in the prevailing wind and current directions. In the regions where the ice floes do not block the coast and where there are open sections of water, as for example at places in the Shantarsk archipelago straits and in the lower sections of bays (Ul'bansk, Nikolai, and Konstantin), the Pacific bearded seal is long confined to the coasts and small numbers can always be seen almost throughout the winter (S. Naumov, 1941). The majority, however, go far away from the coasts and spend the winter and also early spring far away from the Shantarsk Islands. In the northern part of the sea the Pacific bearded seal moves toward the massive drifting ice floes in winter and spring and onto their edges facing the continent (Fedoseev, 1966).

In the second half of spring and early summer the animals are dispersed more extensively with the drifting ice floes but within their food zones, confined to the shallow sections of the sea.

153 A reverse process occurs after the ice thaws, when the seals approach the coasts, quite extensively scattered at first, and then concentrate in the beach rookeries in the same place year after year from August end but mainly in September and October. They remain scattered deep into autumn, at which time the coasts begin to freeze, after which a new cycle of travel of the Pacific bearded seal commences on the ice floes in the sea.

There is a view that one group of the Okhotsk population performs distant migrations in summer and autumn from the southern regions of the sea (especially from Terpeniya Bay) along the eastern flanks of Sakhalin in the north into Shantarsk archipelago. It is these animals, performing distant migrations, that form the coastal rookeries (Tikhomirov, 1961, 1966b). At the same time, there is a reference to the fact that "the Pacific bearded seal moves northward into the Sea of Okhotsk following the thawing ice floes in Tatar Strait" (S. Naumov, 1941). The real situation can only be gauged by studying marked animals.

The seasonal migrations of the Pacific bearded seal in the Bering Sea are evidently somewhat more complex. Its population winters in all probability partly on the shores and partly on the ice edge formed in the extreme northern part of the sea. As the ice recedes southward and the shores are blocked, the fairly well-scattered population also moves with the ice floes southward and ultimately turns up on the edges of the pelagic expanses by early spring (see "Geographic Distribution," p. 174). It is very difficult to establish whether it is the Alaskan population alone or the Chukchi-Anadyr population also that is concentrated in these peripheral sections of ice floes drifting southwest of St. Lawrence Island and southeast of St. Matthew Island. In all probability, both populations

are held there in some proportion but this can only be established with certainty by studying marked animals.

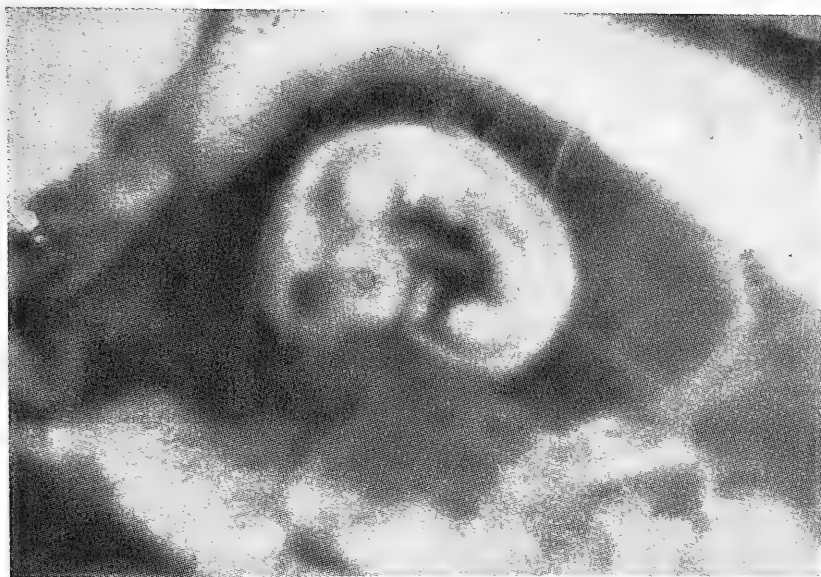
As the summer approaches, the boundary of drifting ice floes with seals begins to shift gradually in a reverse direction northward, to the Bering Strait, with the bulk of the Pacific bearded seals carried along. It is quite possible that a significant part of this population moves northward even farther, into the Chukchi Sea, where it spends the summer in the wide expanses and, possibly, early autumn. The seals, for the most part, are evidently scattered in the coastal belt east and west of the Bering Strait and their return commences in mid-autumn.

A new viewpoint has emerged in recent years on the seasonal migrations of the bearded seal in the White, Barents, and Kara seas. Reports of the wintering of this seal in the White Sea are reliable but the winter range becomes extremely narrow and is restricted evidently only to some small regions. In the southwestern part of the sea such regions are the extreme north of Onezhsk Bay, southwestern sections of the Dvina, and eastern sections of the Kandalaksha bays. Small numbers of these animals, however, winter in all these places. Many more bearded seals winter in Mezensk Bay and in Voronka (V.A. Potelov).

In the Barents Sea this seal winters in the extensive expanses of drifting ice floes in the southeastern part of the sea. It has been assumed that the migratory courses in the spring-summer months diverge in different directions. One leads northeast, along the Novozemel'sk coast to Cape Zhelaniya and probably terminates in the Franz Josef Land archipelago. The other course runs mainly through the Kara Inlet into the western part of the Kara Sea and perhaps extends not only to Baidaratsk Bay and up to White Island, but even farther toward western Taimyr (V.A. Potelov). A reverse movement to the wintering grounds in the Barents Sea occurs in the autumn.

Reproduction. Even 20 to 30 years ago, it was thought that these seals matured in three years and some females even in two years (Sleptsov, 1943). At the end of the 1950s, based on age established from the claws, 154 it became clear that the eastern Canadian female bearded seals attained sexual maturity and conceived for the first time at the age of six years while the bulls became productive at seven years (McLaren, 1958).

The female Pacific bearded seal is the earliest to attain maturity, at the age of three years, but such quick-maturing animals are rare (8% of generation). Mature animals among four-year-olds constitute about one-fifth of the generation but not all the five-year-old females are mature (only 83%); they are all sexually mature only from the 6th year onward. The bulls are all immature at four years of age; 50% attain maturity at



154 Fig. 105. Embryo of a bearded seal. Kara Sea, August, 1965 (photograph by V.A. Potelov).

five years and 66% at six years; all the males are mature only from the seventh year (Tikhomirov, 1966d*).³⁰

Time differences in maturity were detected even in the case of the bearded seal of the western seas of the USSR; 15% of the females of a given generation mature and become fertile at four years of age, over one-half at five and six years, and some individual females at seven years. Males, however, attain sexual maturity earliest, at the age of five years. At six years, over one-half of the males are mature while at seven years, immature animals are quite rare while all the eight-year-old bulls are mature (V.A. Potelov).

Information on the mating season long remained contradictory. From the 1930s, with the availability of information on the behavioral characteristics and based on an analysis of the reproductive organs (Chapskii, 1938; McLaren, 1958), spring, preceding the period of molt and not summer or autumn, was judged as the mating season of the Atlantic subspecies (Wolleback, 1907; Laktionov, 1946). The mating

³⁰ All Pacific bearded seals of both sexes up to five years of age inclusive are regarded as immature in field calculations of growth and weight increments (Kosygin, 1966c).

behavior involves a state of excitation in the animals, which pursue each other, and perhaps "mating calls," recognized as a manifestation of sexual reflexes (Dubrovskii, 1937).

- 155 The bearded seal in the western part of the Soviet range shows intense production of sperm from the second half of March to early July, while ovulation occurs from March end through June but in most animals in the last few days of April. Sperm were detected in the genital tracts of females toward the end of March, in April, and in the first half of May. All this suggests quite an extended mating period (V.A. Potelov).

Errors occurred in determining the mating season of the Pacific subspecies: it was assumed that this seal mated in July (Sleptsov, 1943; Kurcheva, 1955). Observations as well as a study of the reproductive organs showed that the Bering bearded seal also mated in the spring, from April 20 through May 15, mainly in the first 10 days of May (Tikhomirov, 1964). The weight of the testes increases from early March (115 g) to around mid-April (averaging almost up to 190 g) but decreases (to 140 - 150 g) by the second half of May; this weight reduction continues up to early July (Tikhomirov, 1966d*). The different dates of mating and whelping gave rise to different conclusions regarding the duration of the embryonic period. For the Far Eastern subspecies, it was formerly assumed as nine months (Sleptsov, 1943) and for the Atlantic subspecies as roughly 11 months including a lag of embryogeny in the first 1.5 to 2.5 months (Chapskii, 1938; McLaren, 1958).

According to the earlier data, sterility in the Atlantic and Pacific subspecies covered up to 50% of the total eligible females. It was assumed that sterility followed the year of whelping (Chapskii, 1938; Sleptsov, 1948; McLaren, 1958). According to the present data, not more than 25% (V.A. Potelov) or even 20% (Johnson *et al.*, 1966) of the females are sterile every year.³¹ In general, however, the mating period of the Pacific bearded seal has not been adequately dealt with in the literature.

It is significant that mature males are encountered very rarely from April through June in the whelping area of the Bering bearded seal on the sparse ice floes south of the St. Matthew and Nunivak islands. Thus, in 1963, of the 28 animals caught, only one was an adult; in 1964, among the 43 bearded seals caught there, only one was a productive male. More to the north, however, where hummocked ice floes commence, males and females of all ages were caught (Kosygin, 1966b). It is possible, however, that males remained on the St. Matthew and Nunivak islands but lay in the water (animals swimming in the broad water pools between

³¹ An even smaller figure of 10% has been estimated (Tarasevich, 1963).

the ice floes were sighted quite often in 1964) and hence could not attract the attention of the hunters. In any case, the mating period is highly imperceptible. Probably, it proceeds without violent encounters between the competitors, which is quite understandable considering the remarkably peaceful disposition of this animal in general and the absence of any seizure marks whatsoever on the skin of the males.

Some regions of pupping have been identified in the western seas of the Soviet arctic.

Whelping occurs evidently only in the southeastern part of the Barents Sea and in the northern regions of the White Sea. The main region of reproduction in the Barents Sea is the zone of drifting broken ice floes with abundant open water pools between them in the expanse from the White Sea to the Vaigach and Novaya Zemlya islands.³² Beyond the limits of these ranges, whelping is extremely rare. Thus, some stray newborn pups were detected in the central basin of the White Sea (K.K. Chapskii), in the Kara Sea sections closest to the Barents Sea, i.e., in Baidaratsk Bay in the zone of Yugorsk Shar and the Kara Strait (V.A. Potelov). In recent years newborn pups have been found in the White Sea only in Mezensk Bay and Voronka. In Dvina Bay and Gorle, they were nowhere encountered though these regions were surveyed in
 156 March of every year from airplanes and from hunting vessels. No data are available on the finds of conceived or lactating females in Kandalakshsk and Onezhsk bays (V.A. Potelov).

The whelping period in the western parts of the USSR range is confirmed by numerous instances of finding almost completely developed fetuses ready for birth and newborn pups still on the mother's milk. In the White Sea, gestating females caught in the first half of March included fully formed pups which, on being delivered by dissection from killed mothers, could crawl on ice (V. Smirnov,* 1927). One newborn pup was found at Gorle at the end of March, 1947. In the 1960s (V.A. Potelov), new and recently born pups were encountered in the White Sea in the last 10 days of March, in the middle and last 10 days of April, and in the first 10 days of May.

Premature fetuses were found in the Barents Sea on the Novaya Zemlya coasts at March end and in early April, and in the Pechora Sea from the second half of April. Newborns with mothers were noticed in the easternmost part of the Barents Sea from the Pechora Sea to Admiralty Peninsula from the end of the first 10 days of May to the

³² Along the Novaya Zemlya fringe of the Barents Sea, newborns with their mothers were not noticed farther north of the Admiralty Peninsula. Pupping was not reported at all in the Franz Josef Land archipelago.



156 Fig. 106. Fetus of the Pacific bearded seal, *Erignathus barbatus nauticus*, during the process of birth. Bering Sea (photograph by G.M. Kosygin).

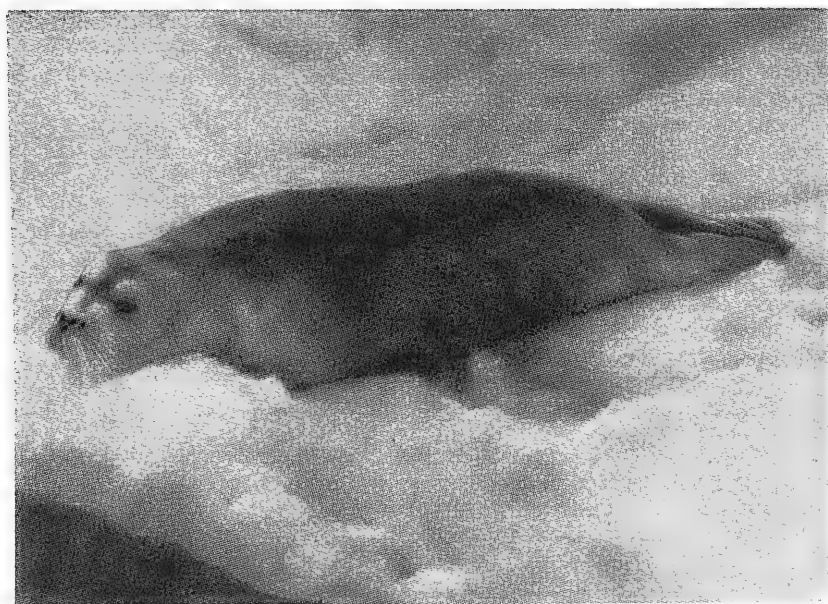
end of the first 10 days of June. Observations in the 1960s covered the whole of April and the first 20 days of May, i.e., the whelping period. Considering that the apparently developed pup was still feeding on milk (i.e., including the entire lactation period), the "pupping period" could be regarded as extending there into the first 10 days of June (V.A. Potelov).

Thus, pups in the western arctic seas of the USSR are born from the last 10 days of March through mid-May, mainly through April, but somewhat earlier in the White Sea than in the Barents Sea where lactation (and hence also whelping) is delayed by at least 10 days.

Information on whelping in the eastern arctic regions of the USSR is extremely vague. The view was expressed that the Kara Sea bearded seals migrated for winter to the Laptev Sea (Rutilevskii, 1939). From this, the conclusion was drawn that the pups were perhaps born east of Taimyr. There is no information on whether the Pacific bearded seal reproduces in the East Siberian and Chukchi seas.

In the Sea of Okhotsk pupping probably occurs everywhere but mainly at places where these seals concentrate (see p. 178) in the spring, i.e., 1) in the western fore-Sakhalin area (including Terpeniya Bay) and 2) in the northern mainland area (mainly the eastern regions, depending of course on the position of drifting ice floes) (Fedoseev, 1971). In general, however, information on the reproduction of the Okhotsk bearded seal, including the conditions and period of whelping, which is
 157 regarded as March end to April, needs to be more accurately established (S. Naumov, 1941; Tikhomirov, 1961; Shustov, 1964). This period (from February through April) for the region of Amakhtonsk Bay is even more indefinite (N.A. Smirnov, 1911). A similar period has been indicated for Tatar Bay also (S. Naumov, 1941). Most of the newborn pups in the Bering Sea appear along the edges of drifting ice floes in the northern part of the sea (region between St. Lawrence and St. Matthew islands and the expanse between the Nunivak and Pribilof islands) and to a lesser extent in the Gulf of Anadyr. The whelping period here is from March end through early May. The peak of whelping here was recorded in the first 10 days of May in 1963 (Kosygin, 1966) (Fig. 107).

In the whelping period the animals are not concentrated in a group as in the rookeries. Instead the whelped females scatter far apart on the



157 Fig. 107. Newborn Pacific bearded seal. Bering Sea (photograph by G.M. Kosygin).

extensive expanses of the drifting ice floes. Thus in 1962, near Novaya Zemlya, on the traverse of the Gulf of Sakhalin and later on the edge of ice floes 50 km away from Matochkin Shar, some 30 females with pups were sighted, lying at 100-300 m away from each other (V.A. Potelov).

The female bearded seal is not particularly choosy about the icy substratum for the newborn. She can make do with an even extremely small portion of a floe or the very edge of a large ice field. The view of some authors (Tyulin, 1938; Rutilevskii, 1939) that whelping occurs possibly under the ledge of an ice floe or under cover of snow in special lairs or holes made by the adult animals in the hummocky piles along the shore ice or far away from it has not been confirmed. Pups everywhere are born in the open. The statement that these seals reproduce on fast ice in the bay and generally on shore ice is equally doubtful (N.A. Smirnov, 1927). The very act of birth has not been observed to date. Evidently it is quite rapid. It was even suggested that the birth can take place not only on an ice floe, but also in the water (Vibe, 1950).

- 158 *Growth, development, and molt.* Until recently, the size of the newborn pup was usually established indirectly by comparing the large fetuses ready for birth. Thus the length of a pup of the Atlantic form at the time of its birth was put at 120-125 cm (in a straight line, *Lcv*) or 130-135 cm (along the dorsal curvature, *Lc*). According to the latest data (V.A. Potelov), newborn pups from the White and Barents seas measure 111-126 cm, average 121 cm (*Lcv*), and 121-141 cm, average 135 cm (*Lc*). The length of the Bering bearded seal at the time of birth was put at 118-137 cm, average 127 cm (*Lcv*); the fetus before birth weighed on average 30.2 kg (G.M. Kosygin).

Fetuses measuring about 100 cm long have a dense pelage consisting of uniformly soft, slightly curled and flattened hairs roughly 15 to 25 mm long. The color is mainly silvery-gray at the base with fairly vivid brown tones in the upper portion. This primary embryonic coat undergoes some changes as the time of birth approaches due to the growth of guard and intermediary hairs and also thinning of the underfur (V.A. Potelov).

The embryonic hair coat is shed partly or even completely in the mother's womb immediately before birth. The newborn has the embryonic hair coat, therefore, only on some parts of the body or this coat has been totally replaced by a new coat. Clumps of matted embryonic fur are found in the womb, in the fetal fluids (as small thickened disks), and also in the intestine of the fetus itself (Bychkov, 1960; V.A. Potelov). The data for the Bering pups do not conform to these observations; these pups are born with a firm hair coat that changes only 2-4 weeks later (G.M. Kosygin).

The molted pup of the Barents Sea resembles somewhat a large, full grown pup of the hooded seal in the color of its skin, but has a

somewhat more vivid silvery luster. The dorsal side is dark gray and the ventral side light steel-gray (V.A. Potelov). Numerous tiny specks and dabs of black or brown are sometimes seen scattered all over the body or just on the front portion and flanks; these extend even onto the head. The characteristic color of the head (light-colored spots) has already been described.

The milk teeth perceptible during development in the womb (Steenstrup, 1860) are preserved in the newborn although in an intensely resorbed form. The permanent upper incisors and canines, as also the second and third premolars, have already cut before birth (G.M. Kosygin).

The lactation period extends for about a month in the western part of our range (V.A. Potelov). In the Okhotsk and Bering seas too this period is nearly similar, terminating in most females in the first 10 days of May according to Tikhomirov (1966a), and in the Bering Sea in the last 10 days of May according to G.M. Kosygin.

There are no detailed reports on the frequency of feeding or on the amount of milk suckled by the pups in one feed. The maximum amount of milk found in the stomach of a pup was 1 liter. The fat level of the milk of the Pacific bearded seal varies from 30 to 60% (G.M. Kosygin) and that of the western bearded seal 26 to 61% (V.A. Potelov and A.G. Beloborodov).

It is difficult to trace the growth intensity during this period. From a comparison of the average sizes of newborn and fully grown pups by the end of May or early June (L_{cv} 140 cm), it is quite evident that during lactation a pup of the Barents bearded seal roughly adds 10-15 cm (the L_c length increases, on average, up to 150 cm).

In the following summer months and early autumn, the pup adds roughly another 5 cm; a yearling measures roughly 155-160 cm (L_{cv}) or 170-175 cm (L_c).

In terms of percentages, the average adult growth dynamics can be expressed as follows: length of newborns about 55% that of fully grown adults; at the end of the lactation period, about 64%; five- to six-month-olds in autumn, 72%; and yearlings, 76%. Six-year-old females in the Canadian population (fully mature by this age) record 91% of their full growth (McLaren, 1958).

The maternal instinct among the seals of this species is quite well manifested. The female spends considerable time on the ice floe near her pup, going into the water to feed only for a short duration. In this period the female cannot make good the loss of her subcutaneous fat reserves; she is highly emaciated and the thickness of the adipose layer has decreased to 3 cm or less by the end of the lactation period. When

people come around, the female sometimes attempts to push the pup into the water and dive with it (Tikhomirov, 1964).

The molting periods are not yet fully understood. In the Kara Sea this period covers July and August (Chapskii, 1938; V.L. Vagin) but its commencement there has not been precisely traced. Much information was reported in the 1960s on the molting of bearded seals in the White, Barents, and Kara seas in an unusually early period. Thus, in the White Sea molted animals began being encountered from the second half of April and early May; in southeastern Novaya Zemlya in the second half of May; in the northern regions of the Barents Sea in June and early July; and in Baidaratsk Bay from early July (and evidently much earlier since fully molted animals were seen at this time) (Potelov, 1967*).

In the southwestern part of the Sea of Okhotsk molting continues from early May through July end (Pikharev, 1940*; Nikulin, 1937; S. Naumov, 1941; Sleptsov, 1943; Kurcheva, 1958*). This period is greatly extended in different regions of this sea.³³

In the northern parts of the Sea of Okhotsk molting proceeds generally at a very late period compared to that in the southern parts where it commences even mid-April (Freiman, 1936). According to recent data, the chronology of molting in the Sea of Okhotsk is as follows: stray molting animals, especially in Terpeniya Bay, were noticed already on April 16; the number of such animals had increased in May and reached maximum in June. Their number was even higher in July but the majority had already molted; nevertheless, some stray unmolted animals were also seen among them (Tikhomirov, 1961).

In the Bering Sea, too, the molting period is extended. It commences with immature animals even in March and April (?; K.Ch.); adults molt mainly from early or mid-May to mid- or end of June (Tikhomirov, 1964; Kosygin, 1966a*).

Enemies, diseases, parasites, mortality, and competitors. Among the large animals that can be reckoned as enemies of the bearded seal in the arctic part of the range, the polar bear has long been regarded as number one. Its stomach often reveals bits of the skin with blubber and sometimes even the whiskers of this seal. The skin of many seals caught in the Kara Sea showed distinct scratches made by the bear's claws. With

³³ Bychkov (1960) reported a much earlier period of molt: among the animals of different ages caught in Terpeniya Bay from March 28 through 31, nine were in a high state of molt (two adult males, two gestating females, and the rest immature animals of both sexes). In six animals intense shedding of hair throughout the trunk had occurred; in two others there were large sections of bare skin on the abdomen and intense shedding of hair on the back; the ninth animal had small clumps of wool only on the neck and around the flippers, while the rest of the body was bare. This pattern of molting is evidently pathological.

the polar bear population reduced at present, the damage caused by it is no longer significant. At places on the coast of the Sea of Okhotsk, during the period of formation of beach rookeries, the Pacific bearded seal suffers also from the brown bear. Seals torn apart by this bear have been seen time and again (on the Moroshechnaya River) and the bare skin of a Pacific bearded seal left behind by a bear was found in the region of Cape Amakhtonsk (Tikhomirov, 1966a).

160 Evidently, young animals are sometimes attacked here and there by the Greenland shark although there are no concrete data to support these events. The damage inflicted by the killer whale is obviously not significant although the stomach of these carnivores caught in the Bering Strait contained the whiskers and claws of the Pacific bearded seal (Zenkovich, 1938*). In exceptionally rare cases, the walrus, too, attacks the bearded seal. At present, however, with the walrus population decreased everywhere (particularly sharply in the western parts of the range in the USSR), the damage caused by the walrus, if any, is practically negligible. Also, there is essentially no trophic competition between these animals. The mollusks consumed by them are varied; while the bearded seal prefers gastropods, the walrus thrives almost exclusively on lamellibranchs. These differences have been strikingly demonstrated in the case of the Greenland-Canadian animals too (Vibe, 1950). At places on the Chukchi coasts, the gray whale, feeding mainly on benthos, is perhaps a competitor of the Pacific bearded seal.

From among the ectoparasites of the bearded seal, especially in the Far East, *Echinophthirius horridus* Olfers (Anoplura) is widely prevalent.

Heavy infection with helminths is reflected far more significantly in the health of this species of animals. Among several dozens of animals inspected even in the 1930s in the Barents and Kara seas (Chapskii, 1938), there was not a single case in which the stomach or intestines did not contain a large number of cestodes and nematodes. Instances are known of the highly diseased state of the animals, with their alimentary canals choked with helminths. As an example, in one animal the intestines, packed with cestodes, were ulcerated at several places to the point of perforation. The animal was extremely sluggish and highly emaciated and there was almost no adipose layer (L. Leonov; August, 1933, Franz Josef Land).

The helminth fauna of the bearded seal comprises 23 species and three larval forms (Delyamure, 1955; V.V. Treshchev, M.V. Yurakhno).

From among the trematodes, *Opisthorchis tenuicollis* parasitizes the bile ducts of the liver. *Orthosplanchnus arcticus*, infecting the gall bladder, bile passages of the liver, and the pancreas, is encountered more often than other trematodes and in much larger numbers. Thus the

liver of the bearded seal can be a host for over a thousand *O. arcticus* (V.V. Treshchev and M.V. Yurakhno). *O. fraterculus* is a parasite of the gall bladder and *Microphallus orientalis* that of the intestines. The cestodes infecting the intestines are: *Diphyllbothrium cordatum*, *D. hians*, *D. latum*, *D. lanceolatum*, *D. macrocephalus*, *D. schistochilus*, *Diplogonoporus tetrapterus*, *Pyramicocephalus phocarum*, and other genera and species of Diphyllbothriidae; a single animal host could harbor up to 44,000 specimens of these parasites (V.V. Treshchev). In some bearded seals the cestodes parasitizing the intestines weigh one-sixth of the weight of the organ itself. *D. lanceolatum* is encountered most often. The nematodes infecting the stomach and intestines are *Contracaecum osculatum*, *Terranova decipiens*, *T. azarasi*, and *Phocascaris phocae*. The heart is infected with *Skrjabinaria spirocauda* and the lungs with *Otostrongylus circumlitus*, and *Parafilaroides* sp. The acanthocephalan worms *Corynosoma strumosum*, *C. semerme*, *C. validum*, *C. hadveni*, and *C. ventronudum* are intestinal parasites.

A comparison of the helminth fauna of *E. b. barbatus* and *E. b. nauticus* revealed, in addition to worms common to both, helminths peculiar to each.

The results of a study of 39 Atlantic bearded seals (V.V. Treshchev) revealed only four which were unaffected while the remaining 35 (89.7%) were infected with helminths and many of them quite heavily. All the animals in the age group of 1 to 15 years were infected. The most frequently infected organs were the stomach (100%), small intestine (100%), duodenum (94.3%), and rarely the pancreas (34.3%) and the liver (22.8%). A single animal could be parasitized by seven species of helminths, more often five, rarely four, six, and even very rarely by three or seven species.

Of the 100 Pacific bearded seals studied (Delyamure and Serdyukov; 161 M.V. Yurakhno), seven were free from helminths while the remaining 93 were severely infected. Parasitic worms were recorded in the various organs of all the animals in the age group 1 to 16 years. Infection of the stomach and the intestines was 100%. The duodenum was often infected (88.1%), less often the liver and gall bladder (48.3%), pancreas (25.8%), and rarely the lungs (2.14%) and heart (1.07%). Parasitism of a single bearded seal varied from 3 to 8 species of helminths. The animals were more often infected by four and five species, rarely by six to eight and more rarely by three species.³⁴

Population dynamics. Because of the lack of population data at any initial level, its dynamics could not be determined accurately. At the end

³⁴ These data were mainly compiled by helminthologists at the Crimean State University under the guidance of Prof. S.L. Delyamure.

of the 1960s, the population evidently rose as a result of the cessation of hunting from ships during the years of World War II and in the early postwar period. The cessation of hunting by Soviet ships in the Barents and Kara seas had a similar favorable impact from the mid-1960s.

The state of the Pacific bearded seal population in the Far East is causing considerable anxiety. Its reduction in the Sea of Okhotsk has been convincingly demonstrated by a sharp reduction in catch per ship. From 1957 through 1963, the average number of Pacific bearded seals caught by a single ship in the southwestern regions of the Sea of Okhotsk decreased from 1,100 to 730, i.e., by one-third. In the southern regions of the sea (in Terpeniya Bay, on the eastern coast of Sakhalin), its population has decreased so much that it has lost commercial importance. Its total catch in the Sea of Okhotsk remained static until the mid-1960s only by extending hunting into the northeastern regions of the sea, in Shelikhov Gulf, where the Pacific bearded seal was formerly almost left alone by hunting ships (Fedoseev, 1966). Simultaneously, its population began decreasing even in the Tauisk-Okhotsk region (Fedoseev and Shustov, 1964). The significant collections of this seal in the beach rookeries of the Shantarsk Islands decreased. While in the 1930s thousands of this seals could be counted in the rookeries, only a few hundred remained by the 1960s. The hunting intensity of the Pacific bearded seal in the Bering Sea should be established with allowance for exploitation of the Okhotsk population.

Field characteristics. The Pacific bearded seal is a large, almost monochromatic (sometimes with large light-colored spots visible from a distance) animal with a relatively small head resting as though directly on the shoulders, without a distinct neck. Light-colored dense and luxuriant whiskers and relatively short, broad fore flippers, as though truncated, are typical features. It is usually seen singly on ice floes and in water. Encountered mainly on the coasts and in shallow waters in winter and in spring, usually beyond the shore ice and among drifting ice. While diving, its back is usually exposed and even the hind flippers on occasion. The flippers and the air holes of the Pacific bearded seal are considerably larger than those of the ringed seal. (K.Ch.)

Economic Importance

In the seminatural rearing of the local coastal population, the Pacific bearded seal plays an extremely significant role in the European and Western Siberian North (mainly for the Nenets population) as well as in the Far East (in the coastal Chukchi-Anadyr region, Koryak coast and coasts of the Sea of Okhotsk). This valuable hunting target causes

no damage to the fishing economy. It is caught for its strong and thick valuable hide, blubber, and meat. Its hide is a superior raw material used locally for making soles of shoes, belts, etc. The skin (of fetuses before birth) with strong well-preserved fur is used locally for making fur goods. The skin of newborns with a strong hair coat is also sometimes used. Compared with that of other seals, the meat of the Pacific bearded seal contains the least blubber and is used at places even for human consumption. Mainly, however, it is used by the collective and state farms for feeding caged animals. The liver is toxic.

An adult animal, on average, yields 20 to 25 kg of hide (thickness about 10 mm and area about 1.7 to 2.0 m²); for local needs the skin is cut by cross "rings" into strips 60 to 75 m long with a width (in raw form) of 2.5 to 3 cm.

The blubber weighs 75 to 125 kg in the summer when the animals are least fed and the thickness of the fat layer averages about 4.5 to 5.0 cm. In the autumn-winter period a single adult yields up to 150 kg or more of blubber. The meat of an adult without viscera often weighs 100 to 160 kg or more.

The popular method of catching is to shoot an animal resting on an ice floe or sometimes showing above the open water. For this purpose, a masked hunter in a whaleboat, motor boat, or canoe slowly edges toward the animals among drifting ice floes or lies in wait with a rifle along the edge of the shore ice. At places, mainly in autumn, the animals are caught in a net. From the second half of summer, the animals are killed in the coastal rookeries by beating them with sticks, as in the case of the *larga* (p. 368).

Presently, the bearded seal is caught in the largest numbers in the Sea of Okhotsk and the Bering Sea from ships which hunt for different types of seals among the drifting ice floes. In the Sea of Okhotsk, until the mid-1960s, the bearded seal held third place (next to ringed and ribbon seals) among all the seals caught. Its catch there rose particularly from 1957, when 15,000 animals were caught with an average catch of 12,500 animals per annum for several years. These figures do not include a few thousand caught by local organizations (Fedoseev, 1966a). In the Bering Sea hunting of the Pacific bearded seal from ships occupies second place (or shares it with the *larga*) after the ribbon seal.

The western hunting region, i.e., the southeastern part of the Barents Sea, is now of lesser importance; from time immemorial our hunters went there in the spring and later even the Norwegians. At present (1960s), hunting operations are continued only by the Norwegian hunting ships in the eastern regions of the Barents Sea where a few hundred bearded seals are caught every year in the region of the "eastern ice floes". In 1963, 324

animals were caught in this region while 1,239 animals were caught in the "northern ice floes," ³⁵ i.e., in the more western regions at Spitsbergen.

The locals hunt in the coastal zone in the Far East along the coasts of the Chukchi Peninsula, Gulf of Anadyr, and along the Koryak coast, and in the coastal regions of the Sea of Okhotsk, as well as in the west from Kanin to Yamal and to a smaller extent at places in the eastern regions of the Kara Sea and in the White Sea. As a result of such intensive hunting, the Pacific bearded seal reserves in the Far East decreased sharply. To prevent further depletion, hunting was regulated in the Sea of Okhotsk. But hunting of the Pacific bearded seal by hunting ships should be totally banned. The summer-autumn killing in the beach rookeries in particular should be banned. In future, as and when the population of this seal is restored, the nature and volume of its hunting should be fixed strictly in accordance with the use of the raw material and the available reserves; special attention should be devoted to census taking.

In the Bering Sea hunting ships should catch only that proportion of the population as cannot lead to its depletion, and the native coastal population should be involved, especially of the Chukchi Peninsula.

163 In the Barents Sea there is a need in the immediate future for more coordinated hunting activity with the Norwegian expeditions based on combined (or in any case coordinated) studies and rational distribution of hunting quotas and also the institution of common hunting rules. To increase the population in the White Sea, hunting should be banned there (Potelov, 1969).

The entire system of economic utilization of the population of this species should be reorganized. It is futile to catch pups of such a large seal for the sake of fur (pups in the initial months alone are suitable for this purpose). The fur quality of the skin requires further investigation. Also, the quantity of such raw material cannot be significant because of the peculiarities of hunting and the scattered distribution of the animal. It would be more appropriate to use this animal for obtaining meat for animal food, the requirement for which has been steadily rising concurrent with increased fur farming. The skin can be used as raw leather.

It is also extremely important that all countries ban the killing of lactating females and pups in order to promote the normal restoration of the Pacific bearded seal population. No less urgent is the problem of systematizing the hunting and utilization of this seal by the coastal population. (K.Ch.)

³⁵ According to the annual report of the Norwegian Fishing Directorate on Seal Hunting for 1963 (1964).

Genus of True Seals and Ringed Seals³⁶Genus *Phoca* Linnaeus, 1758

1758. *Phoca*. Linnaeus. Syst. Nat. Ed. X, I, p. 37. *Phoca vitulina* Linnaeus.
1777. *Pusa*. Scopoli. Introd. Hist. Nat., p. 490. *Phoca foetida* Fabricius = *Phoca hispida*.
1826. *Callocephalus*. F. Cuvier. Dict. Sci. Nat., 39, p. 544. *Phoca vitulina* Linnaeus.
1844. *Pagophilus*. Gray. Zoology of Erebus and Terror, 3. *Phoca groenlandica* Erxleben.
1864. *Halicyon*. Gray. Proc. Zoolog. Soc. Lond., p. 28. *Halicyon richardi* Gray = *Phoca vitulina richardi* Gray.
1864. *Pagomys*. Gray. Proc. Zoolog. Soc. London, p. 31. *Phoca foetida* Fabricius = *Phoca hispida* Schreber.
1864. *Haliphilus*. Gray. Ann. Mag. Nat. Hist., 17, p. 446. *Phoca vitulina richardi* Gray.
1873. *Histriophoca*. Gill. Amer. Nat., 7, p. 179. *Phoca fasciata* Zimmermann.
1904. *Pagophoca* Trouessart. Cat. Mamm. Suppl.: 287. Substitute *Pagophilus* Gray.³⁷ (V.H.)

These seals are of moderate size or smaller, and are the smallest in the family.

The facial portion of the head is moderately long (distance from the eyes to the nostrils is a little more than the distance between the eye and the ear opening). There is a narrow fringe of bare skin surrounding the nostrils and between them. The whiskers have wavy edges. The first digit or the first and second are the longest on the fore flippers.

- 164 The skull has projecting rounded zygomatic arches and a narrow interorbital space. The length of the zygoma, ignoring the processes, is usually at least double its smallest width. The infraorbital foramen varies markedly in size but in most cases is comparatively small and does not

³⁶ Conforming to the relatively wide scope of the genus adopted in this publication, almost all the true seals of the subfamily Phocinae have been grouped under the genus *Phoca* (see below). (V.H.)

³⁷ After Trouessart, 1904*, some authors (Ognev, 1935; and others) have used and continue to use the generic name *Pagophoca*, considering that the name *Pagophilus* was already assigned to *Pagophila* (birds—polar gull). However, according to Article 56a of the International Code of Zoological Nomenclature, *Pagophilus* and *Pagophila* are not homonyms and there is no need for Gray's substitution of the name. (V.H.)

exceed or only slightly exceeds the maximum diameter of the alveoli of the upper canines.

The nasal processes of the premaxillary bones are more or less wedged between the nasal and the maxillary bones and do not reach the nasal bones or just reach them only in one species (*Ph. vitulina*). The nasal bones are fairly long and relatively narrow. The contour of the tympanic bullae proper (without lobes of the external auditory meatus) when viewed from the lower surface, resembles a triangle with smoothened apices or an irregular oval.³⁸ The bony palate either terminates posteriorly in a deep (more often angular, sometimes oval) notch, or is without a deep notch, or forms a somewhat gentle, often double arc, or even an almost straight transverse line. There is a compact bony longitudinal septum in the choanae (within the palatine bones), or the septum is almost lacking, or it terminates in the anterior or posterior half of the palatine bones, or reaches the edge of the latter (*Ph. groenlandica*).

The upper incisors have laterally flattened roots; the crowns of the second and third premolars usually have additional cusps.

The color of the hair coat varies widely: usually spotted, in two species in the adult state, consists of alternating large contrasting sections of light and dark colors (Greenland [harp] seal, *Ph. groenlandica* and ribbon seal, *Ph. fasciata*) or is totally without spots (Baikal seal, *Ph. sibirica*).

The primary hair coat in which the pups of all the species are born, with one partial exception (in pagophobic members of the common seal, *Ph. vitulina*), consists of long silky and dense wool mostly of a very light color.³⁹ Age-related color changes are characteristic of most species to some extent or the other; they are most distinctly manifest in the Greenland [harp] seal (*Ph. groenlandica*).

Sexual dimorphism is comparatively less prominent: adult males are somewhat larger than the females but are not always distinguishable in color. There are some differences in the skull proportions too.

There is one pair of teats.

The seals vary in ecological relations. Some are confined to the coastal zone and are associated, especially during reproduction and molt, with land while others lead an essentially pelagic life style and are associated with ice, on which they reproduce and molt. For the most part, these

³⁸ Deviations of this characteristic are most common in the ribbon seal.

³⁹ In the case of the Atlantic common seal and its ecological (pagophobic) Pacific counterparts (see p. 355), the juvenile hair is shed in the mother's womb itself, or at the time of birth, or (very rarely) in the first few days after birth.

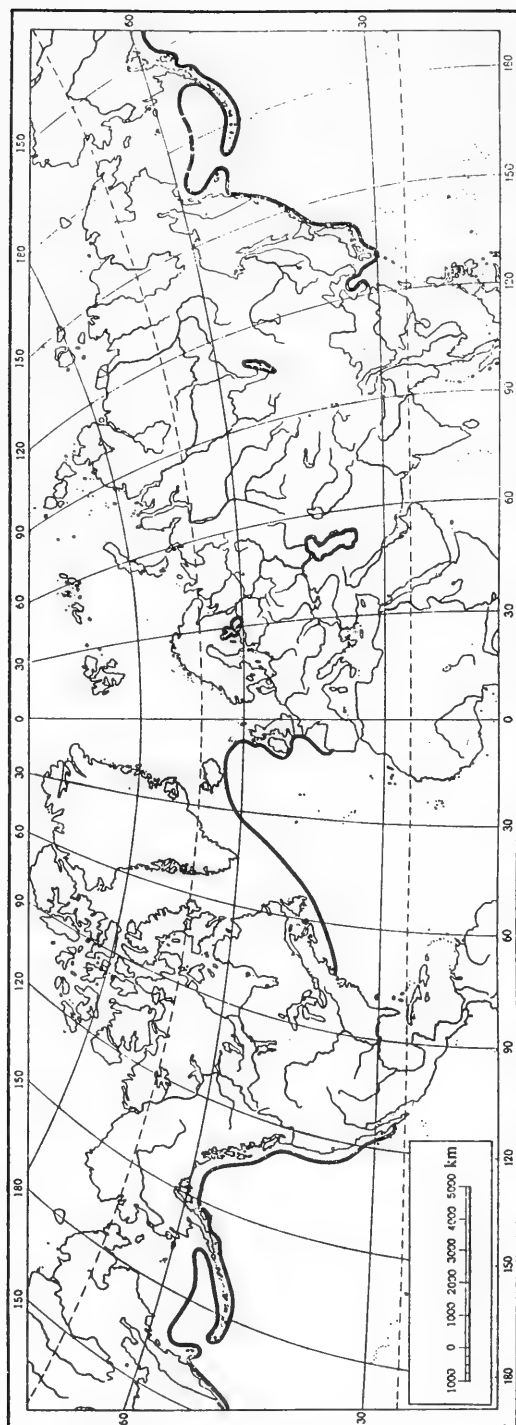
animals live in herds although they remain single during some periods (especially when feeding and, in many species, during the pupping season also). In most of the species, whelping occurs in comparatively narrow limited periods of time, but this period continues from the end of January through July for the genus as a whole. The mating period proceeds without harem formation. There is a latent period [delayed implantation] of 1.5-3 months in the development of the embryo. Mating is followed by the onset of molt and later by a period of intense feeding. Fish and various invertebrates, mainly crustaceans as also cephalopods, serve as food objects. The fatness of the animal exhibits distinct seasonal variation.

The geographic distribution is confined to the arctic and temperate belts of the Northern hemisphere (Fig. 108). Within this zone, the range encompasses the Atlantic, Pacific, and northern Arctic oceans in which the seals are confined mainly to the continental zone; only the Greenland and ribbon seals transgress regularly beyond the continental zone while others do so mainly or occasionally with ice floes. Some species inhabit the landlocked salt- and freshwater bodies (Caspian Sea, lakes Baikal, Ladoga, and some others) and transgress into the lower courses of rivers.

The southern boundary in the Atlantic Ocean along the North American coasts usually does not reach 45° N lat. while the boundary of normal distribution in the European seas does not cross south of Brittany though some rare finds are known up to the Portuguese coasts. In the Pacific Ocean, along the Asian coasts, the distribution zone extends from the Bering Strait to the coasts of Japan (almost up to 35° N lat. on the Pacific Ocean side of Honshu Island), the Korean Peninsula, and even northern China (up to Shantung Peninsula and perhaps even up to the Yantsiyang estuary).

In the Pacific Ocean, on the coasts of America, the range extends down to Cedros Island, Baja California, Mexico (28° 12' N lat.). In the North Atlantic Ocean at least one species of the genus (ringed seal, *Phoca hispida*) inhabits all the peripheral seas, predominantly in the continental terrace (or shelf) zone in the islands and archipelagos directly adjoining the coasts as also away from the mainland, such as Severnaya Zemlya, and the pelagic regions of the ocean. In the Central Polar Basin it extends in rare cases almost up to the North Pole. One or the other species of the genus inhabits everywhere in the seas covering the Soviet coastline with the exception of the Black Sea.

Some species of the genus do not migrate far while others undertake long and regular migrations. A characteristic feature of the latter group is a special, fairly narrow localized region of winter concentration



165 Fig. 108. General range of the genus of true seals and the ringed seal, *Phoca* s. l., including the Greenland seal, *Ph. (Pagophilus) groenlandica* and the ribbon seal, *Ph. (Histriophoca) fasciata* (K.K. Chapskii), southern boundary.

where the seals reproduce and molt and a far more extensive region of summer-autumn habitat (feeding ground) away from the former zone. Not only the seals associated with the coast, but also those related to some pagophilic forms when ice floes in their habitat thaw in summer, form fairly concentrated rookeries on the coasts (large, Caspian seal, partly ringed seal, and Baikal seal).

The origin of the genus has been traced to Miocene ancestors which morphologically are not exceptionally far removed from the present-day species. Thus the sources of the genus extend into even older times. The Pliocene finds (Belgium) help trace the branch quite reliably to the extant species. *Phoca vitulinoides* Bened., *Phoca halitschensis* Blainv., and possibly others also are genetically related to the common seal. The species *Phocanella pumila* Bened. and *Phocanella minor* Bened. lead undoubtedly to the present-day subgenus *Pusa*, a typical representative of which is the ringed seal (*Ph. hispida*). *Callophoca obscura* Bened. from the formations of the same age and place is regarded as a predecessor of the present-day Greenland seal (*Ph. groenlandica*). The center of origin of seals of the genus *Phoca* evidently falls in the Eurasian basin of the Tethys.

The present level of study of the taxonomy of the genus covering generic, subgeneric, specific, and intraspecific diagnosis is quite satisfactory. Nevertheless, further research would lead to a more convincing determination of the volume of the genus, to an accurate diagnosis of the subgenera and species (particularly of the subgenus *Phoca* s. str.), and to a better understanding of the actual intraspecific differentiation of all the species. Much remains vague about the various aspects of ecology, migrations, and population. The ribbon seal, *Phoca (Histriophoca) fasciata*, remained the least studied species until recently, though there is lack of adequate information even regarding other species, e.g., of the subgenus *Phoca* s. str.

The genus consists of six extant species: common seal, *Phoca vitulina* Linnaeus; ringed seal, *Phoca hispida* Schreber; Baikal seal, *Phoca sibirica* 167 Gmelin; Caspian seal, *Phoca caspica* Gmelin; Greenland [harp] seal, *Phoca groenlandica* Erxleben; and ribbon seal, *Phoca fasciata* Zimmermann. This genus is the largest in the family, covering 33% of its species. The significant morphological difference between some of the species has led, and continues to lead, some earlier as well as more recent authors (Scheffer, 1958; Chapskii, 1963; King, 1964) to divide the genus into some, usually up to four, genera. With the broader interpretation of the concept of genus, also adopted by some recent authors (Ellerman and Morrison-Scott, 1961*; and others), it would be more appropriate to regard the natural groups of species as subgenera. Thus the genus comprises four

subgenera: *Phoca* Linnaeus, 1758, covering one species (*Ph. vitulina*);⁴⁰ *Pusa* Scopoli, 1777, with three species (*Ph. hispida*, *Ph. caspica*, and *Ph. sibirica*); *Pagophilus* Gray, 1844, with one species (*Ph. groenlandica*); and *Histriophoca* Gill, 1873, with one species (*Ph. fasciata*).

The species of the genus are almost equally represented in the basins of the Atlantic, Pacific, and Arctic oceans. Three species each are encountered in the first two and four species in the peripheral part of the last. Further, two species are found within the Palearctic in landlocked water bodies: Caspian Sea (*Ph. caspica*) and Lake Baikal (*Ph. sibirica*).

The maximum population of these seals occurs in the arctic seas, i.e., the northern and arctic Atlantic, especially in the polar regions, the Sea of Okhotsk and the Bering Sea, the Canadian-Greenland waters, the Barents and Kara seas, and also the northeastern part of the White Sea.

All the species of the genus are of economic importance to some extent while some represent the most important animals for hunting at sea, especially the Greenland [harp] seal, Caspian seal, ringed seal, and ribbon seal.

All the species of the genus are represented in the USSR fauna: in the Baltic Sea—two species (*Ph. vitulina* and *Ph. hispida*); in the Barents Sea—three species (the above two and the Greenland [harp] seal, *Ph. groenlandica*); in the Laptev and East Siberian seas and also in the Central Polar Basin—one species (*Ph. hispida*); in the Chukchi, Bering, and Okhotsk seas—three species (*Ph. vitulina*, *Ph. hispida*, and *Ph. fasciata*); and in the Sea of Japan (excluding Tatar Strait where three species exist as in the Sea of Okhotsk)—one species (*Ph. vitulina*).

The species of this genus constitute 46% of the total number of species of the order in the USSR fauna and about 1.8% of the total number of species of mammals in the USSR.

In the Soviet territorial and internal waters as well as in the most proximate international waters, the seals of this genus play an extremely significant role in marine-animal-based industries. The Greenland [harp], Caspian, and ringed seals occupy first place in this respect. (K.Ch.)⁴¹

⁴⁰ As a result of recent studies (Chapskii, 1967, 1969), the monotypical state of this subgenus has become extremely doubtful, if not erroneous.

⁴¹ For the key to species of the genus, see under the characteristics of the family (p. 151).

Subgenus of Ringed Seals
Subgenus *Pusa* Scopoli, 1777

RINGED SEAL

Phoca (Pusa) hispida Schreber, 1775

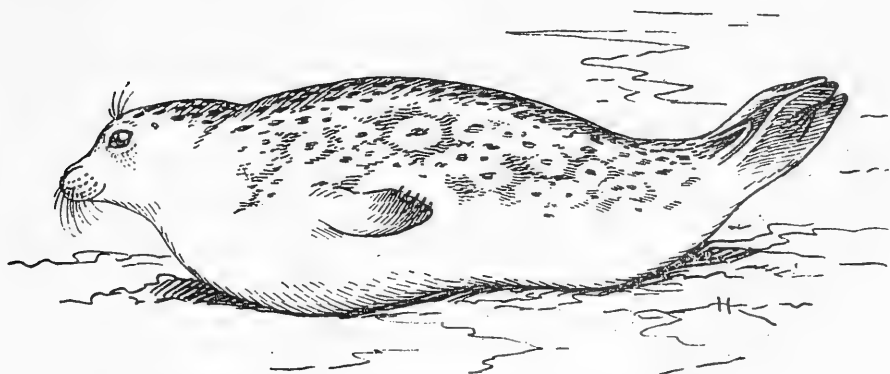
1776. *Phoca foetida*. Fabricius in Müller, Zoologiae Danicae Prodomus, p. VIII, Nomen nudum. Greenland.
1778. *Phoca vitulina botnica*. Gmelin. Linn. Syst. Nat. Ed. XIII, 1: 63. Gulf of Bothnia, Baltic Sea.
- 168 1775. *Phoca hispida*. Schreber. Die Säugethiere, Table LXXXVI. 1776, 3: 312. Northern Atlantic.
1811. *Phoca ochotensis*. Pallas. Zoographia Rosso Asiatica, p. 117. Northern part of the Sea of Okhotsk, between Tauisk and Gizhiginsk bays.
1820. *Phoca annelata*. Nilsson. Scand. Fauna, 1: 362. Renamed *Ph. foetida* Fabricius. Baltic.
1828. *Phoca schreberi*. Lesson. Dic. Class. d'hist. Nat., p. 414. North Atlantic.
1828. *Phoca communis*. F. Cuvier. Dents mamm.
1839. (*Phoca communis* F. Cuvier) B. var. *Octonotata*. Kutorga. Bull. Soc. Imp. Nat. Moscow, p. 189. Neva.
1839. (*Phoca communis* F. Cuvier) B. var. *Undulata*. *Ibid.*, p. 191. Neva.
1899. *Phoca foetida* var. *saimensis*. Nordquist. Acta Soc. Fauna Flora Fenn., 15, 7: 28. Lake Saimaa, Finland.
1899. *Phoca foetida* var. *ladogensis*. Nordquist. *Ibid.*, p. 33, Ladoga.
1902. *Phoca (Pusa) hispida gichigensis*. J. Allen. Bull. Amer. Mus. N. H. 16: 478. Sea of Okhotsk, Gizhiga.
1921. *Phoca hispida pygmaea*. Zukowsky. Arch. f. Naturgesch. 87A, 10: 183. Barents Sea at 77°3' N lat. and 49°40' E long. (pygmy ringed seal); (V.H.)
1929. *Phoca hispida pomororum*. Smirnov. Dokl. Ak. Nauk. (C. R. Acad. Sc.) Leningrad, p. 95. Western coast of Novaya Zemlya.
1929. *Phoca hispida pomororum natio rochmistrovi*. Smirnov. Dokl. Ak. Nauk. (C. R. Acad. Sc.) Leningrad, p. 95. Sumsk environs, Onezhsk Bay, White Sea.
1929. *Phoca hispida birulai*. Smirnov. Dokl. Ak. Nauk. (C. R. Acad. Sc.) Leningrad, p. 96. Lyakhov Island, Novosibirsk Islands.
1935. *Phoca hispida krascheninnikovi*. S. Naumov and Smirnov. N. A. Smirnov, V. Adlerberg, Vinogradov, Smirnov, Flerov. Arctic Animals. Leningrad, 1935. Bering Sea. (V.H.)

Diagnosis

The body length, including the tail, along the dorsal side (*Lc*) is not more than 175 cm and the condylobasal length of the skull not more than 200 mm. The main background color of the hair coat on the upper side of the body is dark, broken by a network of light-colored streaks, mostly in the form of oval ringlets. The skull has a highly shortened rostral portion: its length up to the commencement of the orbit is shorter than the orbit (Fig. 89); the second to fourth lower premolars and molars bear accessory cusps diverging from the base. The interorbital space is very narrow (usually not wider than 7 mm in adults). The tympanic bullae are relatively large, their length exceeding the gap between them, while the width of the bony lobe of the external auditory meatus is more than the distance between its anterior edge and the crest of the articular fossa. The anterior edge of the nasal bones bears three minute denticulate processes. (K.Ch.)

Description

In body proportions the ringed seal resembles the other small seals, i.e., Caspian and Baikal seals. The fore flippers are shorter than the hind ones and the first and second digits of the fore flippers are longer than the third; the claws on them are of moderate size, with moderately elevated upper margin, usually without such a narrow and high crest as in the claws of the Baikal seal. The head has a shortened snout (Fig. 109). The labial whiskers are flattened and have wavy edges. The total number of them (on each side) varies from 42 to 59; the supraorbital whiskers number 3 to 6 and those near the nostrils one each. (Yu.I. Nazarenko)



169 Whitish gaps on a dark background, seen prominently in the form of fairly distinct ringlets or curved streaks, are characteristic of the coloration of the hair coat. The distribution of these streaks in different parts of the body surface is not very uniform. This pattern is most distinct and constant along the edges of the back and on the flanks but absent throughout the entire median narrow zone of the back. It is also absent on all the flippers and sometimes even on the ventral side which, in most members of the population, is generally much lighter than the back. In the anterior portion of the body, up to the shoulder blade and the fore flippers, the ringed pattern is usually extremely fine and alternates with light-colored variegations of different sizes and shapes. The arrangement, size, shape, degree of clarity, and width of the rings vary notably. They gather mainly along the edges of the back in wavy rows like a typical network. Isolated ringlets scattered in different sections of the upper side of the trunk are also seen. Sometimes the ringlets are fused in twos, threes or more.

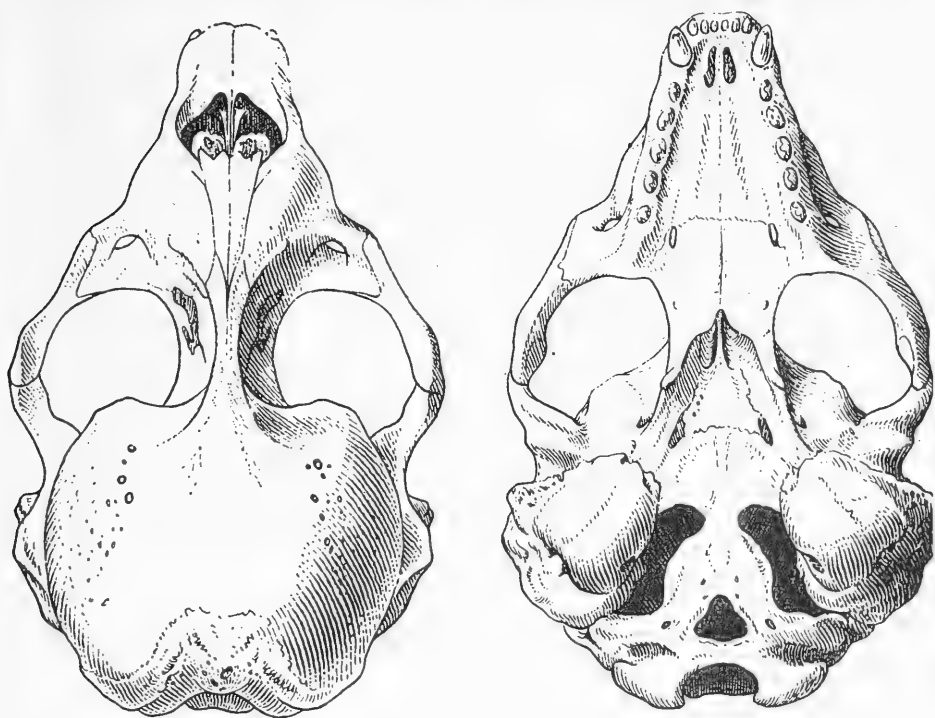
The main background color on the dorsal side varies from a olive-gray to almost black. The ventral side in most of these seals is lighter in color. When the color is uniformly vivid over the body, the underside is generally slightly lighter because of the more intensely manifest and diffuse ringed pattern (large number and greater width of the ringlike streaks). When the dorsal side is darker than the ventral side, the color on the flanks varies gradually. The rings are more often stretched along the body length, slightly curved, and generally irregular in shape, especially when the maximum number are crowded as though woven into a net. Isolated clear zones are usually rounded and uniform. Their longitudinal diameter does not exceed 10 cm, usually much less. In very rare cases the ringed pattern is indistinct, dull, or lost altogether. These clear zones become very small and disappear toward the head and the tail.

The upper side of the fore flippers is of the color of the adjoining part of the body, sometimes with minute brownish specks or dabs. The axillary portion is lighter in color. The color of the hind flippers is almost monochromatic, dark, usually slate-black.

The color details of the hair coat, i.e., the ringlike pattern (number, distribution, and degree of sharpness of contour of circular clearances, their shape and size) and the main background color vary widely in different animals. Animals with a very bright or dull annular pattern are also encountered; some have many rings forming a somewhat circular pattern while these are few and isolated in others; the rings are sometimes large, sometimes small and light-colored streaks forming them are not always closed; sometimes they are thick and sometimes narrow and their shape varies from nearly circular to oval; sometimes the rings are

170 highly elongated as though fused. There are no significant age-related color changes (apart from the replacement of the embryonic pelage in the pups). There are fewer ringlike streaks of light color on the skin of pups, especially in their first year (after the first postnatal molt). Sex-related color differences are absent.

The skull has a highly enlarged cranium, short and narrow snout, and narrow interorbital space (Fig. 110). The width of the cranium immediately above the mastoid processes exceeds its length measured from the orbits to the posterior edge of the occipital condyles. The width at the zygoma in most cases is nearly the same as the skull width at the mastoid processes, sometimes perceptibly exceeding the latter. In adults the length of the auditory bullae not more than their width, constitutes 20-23% of the condylobasal length. The anterior margin of the nasal bones has three denticulate processes while the width of these bones at the point of wedging into the frontals constitutes 15-20% of their total length; they are wedged into the frontals to one-third to half of their total length. The posterior margin of the bony palate is bracerlike or has a simple angular notch, or, in rare cases, is smooth. The longitudinal



bony septum in the choanae runs posteriorly not beyond the anterior half of the longitudinal palatine suture.

The teeth, including the canines, are relatively thin and small. The upper premolars, commencing from the second, usually have a single accessory cusp anteriorly and another posteriorly; rarely, the anterior accessory cusp is lacking or there are two accessory cusps posteriorly. The second to the fourth lower premolars have a split fanlike crown which usually has one accessory cusp anteriorly and two posteriorly. The upper molar usually has three cusps while the lower one often has four; gaps between the molars from the upper first to the fourth are usually present.

The difference in the cranial dimensions of males and females is slightly in favor of the former; differences are seen in the length and 171 various dimensions of the skull width. Age-related variations, however, fall in the general pattern (see p. 221).

The diploid chromosome number is 32.

The body length of adults measured from tip of nose to tail end along the dorsal curvature (L_c) varies widely in different populations, individually and geographically, depending on age and sex, from 101 to 125 cm, possibly even more. The feeding conditions of the juvenile, which evidently leave a mark on its entire life, play quite an important role on the body length. The newborns which, for some reason or the other, are underfed, remain far from attaining normal size by the time they reach sexual and complete physiological maturity and quite often remain puny. The body length of such pygmy seals differs little from that of young ones.

The overall weight of the adults varies in different populations from 30 to 80 kg and, in the largest and well-fed animals, especially among the Baltic ringed seals, the males can weigh up to 133 kg and females 125 kg (V.A. Zheglov). In the western arctic USSR the average weight of adult males is 56.3 kg, of females 53.2 kg.

The relative weight of the internal organs (as percent of total body weight) in Bering ringed seals weighing 24-32 kg was as follows (g): heart 23-87; liver 22-43; and lungs with trachea and larynx 9-22. The weight indices of these same organs in Ladoga ringed seals weighing 30-42 kg was: 47-105; 15-41; and 215-238. The small intestine was 14.7 m long (Sokolov, Kosygin, and Tikhomirov, 1966).

The skull measurements of males from the eastern regions of the Barents Sea and western part of the Kara Sea⁴² were: condylobasal length 161.5-182 mm; mastoid width 96.5-108.5 mm; width at the

⁴² According to the data of the Zoological Museum of Moscow University.

zygoma 94-109 mm; width at the upper canines 22-28.5 mm; and interorbital width 3.8-6.2 mm. The skull measurements of females (from the same regions) were: condylobasal length 159-173 mm; mastoid width 95-109 mm; width at zygoma 99-105 mm; width at the upper canines 22-29 mm; and interorbital width 4-7.3 mm. The dimensions of ringed seals within the USSR reveal significant geographic variation (see pp. 231-234). (K.Ch.)

Taxonomy

Taxonomically, the ringed seal is most closely related to the Baikal (*Phoca sibirica* Gmelin) and Caspian (*Phoca caspica* Gmelin) seals along with which it forms the subgenus *Pusa* or the true seals. Some authors have assigned this subgenus the rank of genus (Scheffer, 1958; Chap-skii, 1963; King, 1964). Concomitantly, attempts were also made to classify *Ph. sibirica* and *Ph. caspica* only as subspecies of *Ph. hispida*, a view that did not find favor. Among the other extant members of the genus *Phoca* s. l., the common seal or larga (*Phoca vitulina* L.) is closest to the ringed seal in systematic position and evolution. Sometimes the two are combined under a single subgenus. Both the subgeneric (or generic) branches have been identified at least from the Upper Miocene.

The interrelations between members of the group *Pusa* are not yet entirely clear. The prevailing view is that the ringed seal is closer than all the others to the original ancestor in the line from which the two other closely related species evolved by some type of invasion from the north and isolation in landlocked reservoirs at a very early stage of its geological history. Another view holds that the primary subgeneric branch evolved in a more southern landlocked sea derived from the Tethys, if not in the Tethys *per se* (Chap-skii, 1968).

- 172 A morphological comparison points to a closer affinity of the ringed seal to the Baikal seal rather than to the Caspian seal though a crosscheck of the craniological features reveals a fairly variegated picture (Chap-skii, 1955b). (K.Ch.)

Geographic Distribution

Covers the peripheral seas of the polar basin, rarely its central regions, the arctic and subarctic Atlantic seas, the northernmost and northeastern parts of the Pacific Ocean (Bering Sea and the Sea of Okhotsk), Baltic Sea, Lake Ladoga, and the Saimaa lake system.

Geographic Range in the USSR

Accounts for no less than half the total range of the species. In the seas of the arctic belt the distribution of the ringed seal extends continuously from the western to the eastern boundaries of the USSR (Fig. 111).

It inhabits the southern, eastern, and northern marginal portions of the Barents Sea, encompassing the belt of ice floes from Novaya Zemlya to the meridian of Spitsbergen, but is not reported from the pelagic central and western parts of the sea. The boundary of the range in this sea runs close to the Murman shores in the east, turns then to the south of the White Sea Inlet, turns arcuately roughly from the meridian of Cape Kanin Nos to the northeast and, having reached roughly the latitude of the northern extremity of Novaya Zemlya, turns westward. In the coastal waters of Murman it is distributed almost everywhere with a preference for sections with a more rugged coastline quite protected from the surf, especially river expanses in estuarine zones. It may be assumed that the ringed seals present on the coasts of western Murman represent recent arrivals since suitable biotopes for breeding are not available there.⁴³

The range in the White Sea covers all the bays except the inlets and straits. The ringed seal often swims into the lower reaches of the rivers. In Dvinsk Bay it is distributed almost everywhere in the peripheral zone in the south to the very mouth of the Northern Dvina but is evidently scarce in its northwestern open part as also in the Central Basin. It is quite common almost everywhere in Kandalaksha Bay, right up to its uppermost (cul-de-sac) part; in the central regions of the bay, however, it is sporadic. It is obviously confined to the northern half in Onezhsk Bay as also in its western regions abounding in islands and with a particularly rugged coastline.

It is quite common in Mezensk Bay but prefers the coastal belt. On the whole, the distribution in the White Sea is quite extensive but it usually avoids the extreme central portion of the sea and the straits away from the coasts. This is true of the summer-autumn as well as winter-spring period. In summer it is common even in the northern

⁴³ Scant, fragmentary, but nevertheless concrete information on the distribution of the ringed seal on Murman coasts is scattered in the works of Pleske (1887), Knipovich and Yagodovskii (1902), Knipovich, Yagodovskii, and Zhikharev (1902), Soldatov (1902), Breitfus (1903, 1905, 1912, 1915), N. Smirnov (1903), Wolleback and Knipovich (1907*), Formozov (1929), Sdobnikov (1933*), and Surkov (1965*).

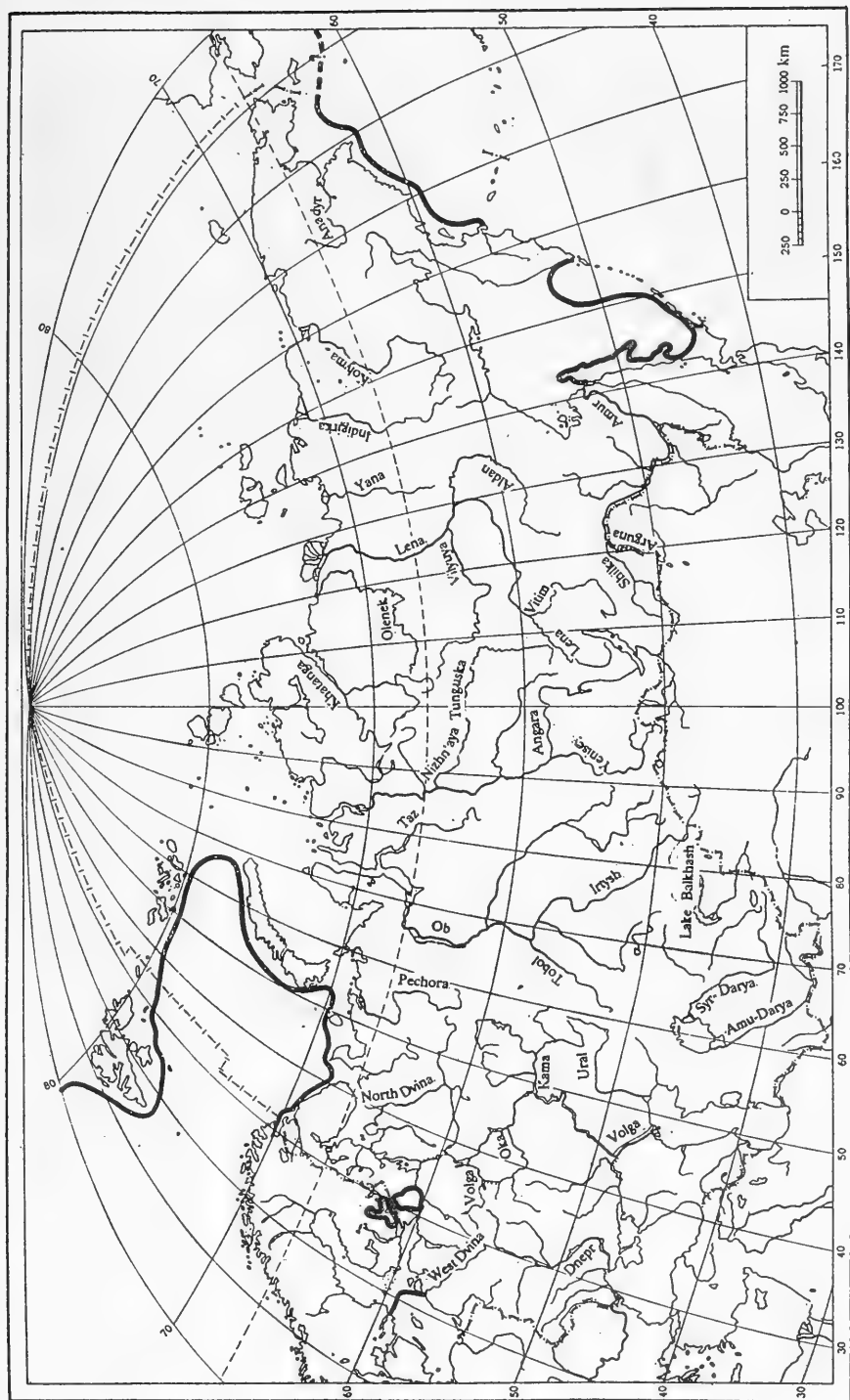


Fig. 111. Range of the ringed seal, *Phoca hispida* in the USSR (K.K. Chapskii)

regions of the White Sea and forms rookeries there⁴⁴ on the bars and spits. In the eastern inlets of the White Sea the ringed seal inhabits the Kanin-Kolguev shallow waters, Cheshsk Bay, the Timansk coastal waters and the Pechora Sea up to Yugorsk Shar, Vaigach, Kara Strait and southern parts of Novaya Zemlya inclusive, with a preference for peripheral coastal expanses.⁴⁵

In the more northern regions of the eastern extremity of the Barents Sea, the distribution extends in a strip that is not very broad along Novaya Zemlya up to the latitude of its northeastern extremity. Here the ringed seal is confined preferentially to the bays, especially those which project deeply into the land with highly rugged coasts, and not to the open spaces or capes jutting into the sea. It also inhabits Matochkin Shar.⁴⁶

From the northeastern extremity of Novaya Zemlya the boundary of distribution turns northwest and extends through the zone of drifting ice floes into the region of Franz Josef Land archipelago. Here and in its immediate icy environs the ringed seal is quite common and is found almost everywhere. It is particularly numerous in the straits in summer but not sighted in winter, evidently because concealed by the ice cover.⁴⁷

The completely isolated Baltic portion of the range of the ringed seal covers the regions of all our territorial waters in the Gulf of Finland including Nevsk Bay (where, however, it is rare), the region of Sarema and Hiiumaa islands from the contiguous strip of the Baltic Sea itself, extending northwest, and also the entire Gulf of Riga.⁴⁸

Lake Ladoga constitutes a distinct section of distribution.

⁴⁴ Some data of a very special nature on the distribution of the ringed seal in various regions of the White Sea were drawn from Danilevskii (1862), Knipovich (1897, 1907*), Zhitkov (1901, 1904), N. Smirnov (1903), V. Nikol'skii (1927), Bianki (1965), Golenchenko (1961, 1963*), Nazarenko (1967, 1968), and others. The unpublished data of A.P. Golenchenko, Yu.I. Nazarenko, V.A. Potelov, and others were also used here.

⁴⁵ For the characteristics of distribution of the ringed seal in the southeastern regions of the Barents Sea, data from the following published and unpublished sources were used: Golenchenko (1961), Zhitkov (1903*, 1904, 1913), Klumov (1935), Moskalenko (1945), A.P. Golenchenko, Yu.I. Nazarenko, V.A. Potelova, Tsapko (1958*), and others.

⁴⁶ Based on the published and unpublished observations and information of several researchers: Krivosheya (1884), Gorbunov (1929), Lepin (1935*), Klyuge (1936), M.I. Vladimirskaia, A.P. Golenchenko, A.N. Dubrovskii, A.I. Zubkov, V.A. Potelov, and K.K. Chapskii.

⁴⁷ More detailed information on the distribution of the ringed seal in the Franz Josef Land archipelago can be found in the works of Nansen (1901*), Al'banov (1917), Pinegin (1934*), Esinov (1935), and Tsalkin (1936). The oral communications of L.I. Leonov, hunters, and others were also used here.

⁴⁸ This general review of the distribution of the ringed seal in the Baltic was drawn mainly from the works of Greve (1906*), Schubert (1929), Freund (1933), Ropelewski (1952), Aul, Ling, and Paaver (1957), Bergman (1960*), Leis (1960), and V.Z. Zhiglov.

The distribution of the ringed seal in Lake Ladoga changes depending on the time of year, ice drift, and finally on the migration of some of its food objects. In summer and autumn the seals confined predominantly to the coastal zone go farther away from the coasts in winter, especially in the shoals; in spring they may be transported even into the central portions of the lake together with drifting ice floes. In summer and autumn these seals are concentrated at places in the immediate proximity of the coast or toward the islands and rest on individual boulders, rocky "ludas" [littoral shoal or islet], and sand bars.⁴⁹

In the Asian sector of the arctic the southern boundary of the range runs all along the coast of Western and Eastern Siberia to the Bering Strait. Northward, however, the range extends up to the Central Polar Basin (Chapskii, 1949; Rutilevskii and Uspenskii, 1957). A more complete picture of the distribution of the ringed seal is available for the Kara Sea. Here it is found everywhere to some extent but preferentially in the coastal belt, from Novaya Zemlya to Vil'kitsk Strait and Severnaya Zemlya. On the eastern coasts of Novaya Zemlya, it is distributed, although not very uniformly, all along the stretch from Cape Zhelaniya to the Kara Strait. Southeast of the latter, it inhabits the coastal belt of Vaigach and Yugorsk Shar. It inhabits Baidaratsk Bay and the western coast of Yamal. The central regions of this part of the sea also fall into the range since the ringed seal is encountered there at different places along with ice floes, at least in the summer season. Farther east, it inhabits Malygin Strait and generally the waters of White Island, Gulf of Ob with much of Tazovsk Bay, the expanse from Shokal'sk Island to Yenisey Gulf (including Gydayamsk Bay), the region of Dixon Island, Pyasinsk Bay, and the coastal belt of western Taimyr to Vil'kitsk Strait. Along the western rim of Severnaya Zemlya, the range rises to its northernmost extremity and runs far northward. The ringed seal is encountered on all the islands of the Kara Sea, even such islands as Uedineniya and Vize⁵⁰ which are far away from the continental coasts.

⁴⁹ The distribution of the Ladoga seal has been described from the data of Chapskii and co-authors (1932*), Golenchenko (1935), N. Smirnov and colleagues (1954*), Sorokin and co-authors (1957, 1958*), A.S. Sokolov (1958*), A.A. Antonyuk, A.I. Zubov, P.V. Fil'kin, and others.

⁵⁰ This summation of the distribution of the ringed seal in the Kara Sea is based on the observations of several individuals and on data from the literature, including Zhitkov (1913), Heptner (1930, 1936), S. Naumov (1931), Kolyushchev (1933), Probatov (1933), Klyumov (1935), Urvantsev (1935), Kirpichnikov (1937), Mikhel' (1937), Chernigovskii (1935), Antipin (1939*), Rutilevskii (1939), Laktionov (1947*), Ushakov (1953), Mikhailov (1958), G.G. Galkin, L.I. Leonov, V.F. Nikitin, V.A. Potelov, A.N. Tyulin, K.K. Chapskii, I.K. Yaki-movich, and others.

Information on the ringed seal in the extreme east is highly incomplete. It is quite widely distributed in the Laptev Sea though very unevenly, as in the western part, close to the coast of eastern Taimyr (on Komsomol'sk Pravda Island, in Faddei Bay, and in the Pronchishcheva Bay region), in Khatanga Gulf, in the region of Begichev Island, and in Nordvik Bay, and very far in the east along the coastal strip. It is encountered even in the bays of such rivers as the Anabar, Olenek, Lena, and, in the more northern regions, especially in the eastern part of the sea, on the threshold of the Dmitrii Laptev and Sannikov straits, and in the zone of the Novosibirsk Islands. More than at other places, ringed seal sightings are reported from the region of Begichev Island and southwest of it (Koshkin, 1937). In general, however, this sea is regarded as far from abounding in ringed seals (Mikhel', 1937).

In the East Siberian Sea the ringed seal inhabits the coastal belt and evidently all the bays, estuaries, and foredelta sections as well as the pelagic regions of drifting ice floes; it reaches the Novaya Siberia and De Long islands. In the western regions of the sea, west of the Medvezhii Islands, the ringed seal is considerably less numerous than east of the Kolyma estuary; it is most numerous in Chaunsk Bay and the adjoining coastal belts. It was encountered, though not often, in the more northern pelagic regions, including in the proximity of Wrangel Island.⁵¹

It is common in the Chukchi Sea along the entire coastal belt but because of the shallow waters, it is quite often confined more toward the open sea. Its most abundant regions are near Cape Serdtse-Kamen', Kolyuchin Bat Inlet, and northwest of Kolyuchii Island (Fedoseev, 1965c). The northern boundary of distribution in the Central Polar Basin is not amenable to precise determination. It is drawn (Scheffer, 1958) tentatively along 85° lat. but innumerable cases of the appearance of ringed seal are known even more northward, even at latitudes 88° and 89° or a few minutes farther away (Chapskii, 1949; Uspenskii and Rutilevskii, 1957*). The entire Central Polar Basin should perhaps be included in the range of this species though the ringed seal is extremely rare in the fore-polar regions and is seen evidently only in the spring-summer months.

In the Far Eastern waters, south of the Bering Strait, the range of the ringed seal encompasses the entire mainland rim of the western part of the Bering Sea. On the eastern and southern coasts of the Chukchi Peninsula, the ringed seal is extremely common and numerous and is most concentrated in winter and spring in a wide belt of coastal ice floes

⁵¹ According to the data of Iokhel'son (1898), Buturlin (1913), Arsen'ev (1935), Mikhel' (1937), Fedoseev (1966b), and others.

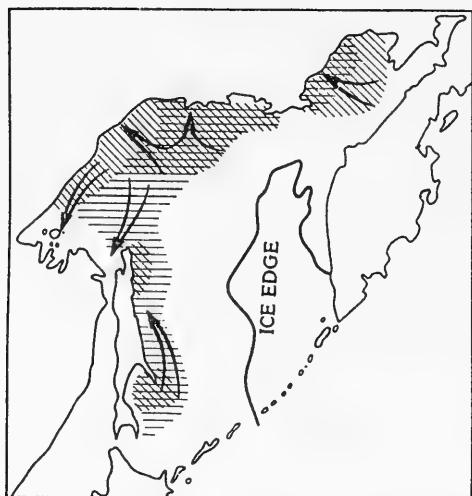
all along the stretch from Cape Dezhnev to Provideniya Bay and farther west in the regions of Rudder Spit and especially Krest Bay (Fedoseev, 1965c). The ringed seal is also common in the Anadyr drowned river valley [Gulf of Anadyr] and the surrounding coastal waters; it often transgresses in summer into the lower courses of the Anadyr and other rivers, sometimes even extremely small rivers and rivulets; it is seen moving along the Gulf of Anadyr coasts, remaining long and even wintering at places in the bays, straits, and on open beaches (Portenko, 1941; 176 V.N. Gol'tsev). It is encountered, though less numerous, on the Koryak coast (N.B. Shnakenburg).

Southwest of Cape Olyutorsk, the ringed seal inhabits the entire coastal belt, descending to Apuka, Il'pi Bay (Anastasia), Parapol'sk Valley and Karaginsk Island, and the eastern coast of Kamchatka (Samorodov, 1939; Averin, 1948; L.A. Portenko and F.B. Chernyavskii). It has been reported from time to time in the sea, far away from the land, mostly in the season of drifting ice floes. In the Bering Sea the ringed seal usually inhabits only the coastal zone (Rozanov, 1931; Razumovskii, 1933; Shustov, 1967, 1968*; E.A. Tikhomirov; and others). This is also confirmed by the 1964 observations of K.K. Chapskii.

It is extremely difficult to draw the boundary of distribution in the open sea beyond which the ringed seal does not enter the south and the east. The mean position of the ice edge in the winter-spring period can partly and only tentatively serve as such a boundary line. Only in the proximity of the continental coast does the boundary descend to the latitude of the Commander Islands ⁵² (Barabash-Nikiforov, 1935*; Marakov, 1964*, 1968); still more southward, in the coastal zone of Kamchatka, it barely reaches Cape Lopatka along the eastern coast. A find on the northernmost edge of the eastern side of the Kuril Range is quite difficult to explain.

The distribution of the ringed seal in the Sea of Okhotsk covers the entire northern part of the sea in a broad belt from west to northeast, from the Gulf of Sakhalin and the Shantarsk Sea up to Gizhiginsk and Penzhinsk bays more deeply projecting southwest, and also the Tigil'sk region and the adjoining sections slightly south of western Kamchatka. From the outer edge of this strip along the eastern edge of the sea, along the eastern coast of Kamchatka, the range arcs into a somewhat less broad strip southward and comes to naught on the northern islands of the Kuril range. In the southwestern part of the sea, however, the space covered by the ringed seal extends in a broader strip along Sakhalin up to

⁵² On the Commander Islands themselves, "random finds of stray animals" (including gestating females) have been reported at various points on the coast (Marakov, 1968).



176 Fig. 112. Distribution of the Okhotsk ringed seal, *Phoca hispida ochotensis*, in the breeding period and its migratory course for molting in the Sea of Okhotsk (cross-hatching) and in 1969 (horizontal hatching) (G.A. Fedoseev).

its southern extremity and up to the southern Kuril Islands. It is difficult to draw the exact boundary of distribution in the central pelagic regions of the sea since this depends to some extent on the movement of ice floes and is therefore extremely variable not only in the course of the annual cycle, but also from year to year. It could be represented schematically as slightly receding northwest of the long-time mean position of the winter ice edge. As a result, the southern boundary of distribution in the Sea of Okhotsk runs along a fairly steep arc whose curve faces northwest, with one end approaching almost the northernmost and the other almost the southern Kuril Islands.

In the Sea of Japan the ringed seal inhabits only Tatar Strait, entering it in the south roughly up to the latitude of De Kastri or slightly more southward (Dorofeev, 1935*).

177 *Geographic Range outside the USSR*

In the arctic and North Atlantic Ocean the ringed seal occupies the northern regions of the Norwegian waters (usually this is the Finnmark region but in particularly cold years the boundary shifts to Lofoten or more south), Spitsbergen archipelago and the strip of arctic pack ice in the west up to the coastal waters on the eastern side of Greenland, and in the north almost up to 75° N lat. Farther west, the range covers the strip along the western coast of Greenland in the north to Kane

Basin inclusively, the Labrador coast, northern edge of Newfoundland, the northernmost part of St. Lawrence Bay (in the south up to 50° N lat.), almost the entire Canadian archipelago, Hudson Bay, and Hudson Strait (Fig. 113).

In the Baltic Sea Basin the distribution covers the Gulf of Bothnia, the zone of Åland Islands, the Baltic Sea proper adjoining this zone, and the entire northern part of the Gulf of Finland west of the USSR boundary. Lake Simaa in Finland represents an isolated section.

East of the Bering Strait, the distribution covers the eastern part of the Chukchi Sea and southern regions of the Beaufort Sea; in the Bering Sea it covers the northeastern extremity of the Bering Sea adjoining Alaska, and to the south up to the northern edge of Bristol Bay. In the Sea of Okhotsk the distribution includes the northern coastal waters of Hokkaido. (K.Ch.)

Geographic Variation

The extensive but fragmented distribution of the ringed seal suggests a fairly significant intraspecific geographic variation. Soviet waters are host to six subspecies (N. Smirnov, 1929, 1935; Ognev, 1935). At present, due to lack of adequate conclusive proof, not all are recognized (Chapskii, 1952). The diagnosis of the entire subspecies should be reviewed afresh with the exception, probably, of the Far East ringed seal, which has been fairly well detailed (Fedoseev, 1965c; Fedoseev and Yablokov, 1965).

The following subspecies have been recognized in the ranges falling within the USSR.

1. Baltic ringed seal, *Ph. (P.) h. botnica* Gmelin, 1788 (syn. *annelata*).

This subspecies is almost the largest in size (V.A. Zheglov). The color is deep dark, often almost black, especially the dorsal background which bears a "lacy" network of light-colored ringlets. The condylobasal length of the skull is 158-187 mm (average 163.2) (Ognev, 1935).

Eastern part of the Baltic Sea and Gulfs of Finland and Riga.

Outside the USSR, it has been reported in the northern, western, and southern parts of the Baltic Sea.⁵³

2. Ladoga ringed seal, *Ph. (P.) h. ladogensis* Nordquist, 1899.

The size is only slightly smaller than that of the preceding subspecies. Proximate in color to the Baltic ringed seal but usually slightly lighter (V.A. Zheglov). The average body length of the female including the tail

⁵³ The greater morphological proximity of the Baltic subspecies to the Ladoga and Saimen subspecies than to the Pomorsk subspecies (White Sea populations) has also been confirmed by the latest craniometric data (Müller-Wille, 1969).

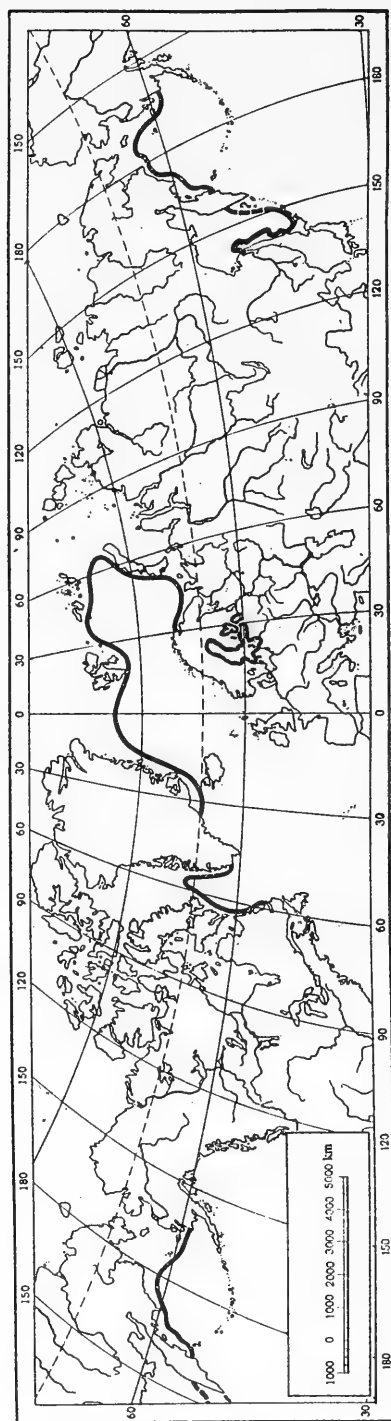


Fig. 113. Range of ringed seal, *Phoca hispida*, southern boundary (K.K. Chapskii).

along the dorsal curvature is 125.3 cm. The condylobasal length of the skull is 167-184 mm (average 173.3) (A. Sokolov, 1956).

Lake Ladoga.

Not reported outside the USSR.

3. Pomorsk ringed seal, *Ph. (P.) h. pomororum* Smirnov, 1929 (syn. *pygmaea rochmistrovi*).

The size is relatively large. The color shows no black tones and the ventral side is usually lighter.

The body length including the tail is 111-153 cm along the dorsal curvature; males average 127.6 cm and females 126.6 cm (Chapskii, 1940). The condylobasal length of the skull is 167-189 mm ($\bar{x} = 177.2$) (and even 201) (Ognev, 1935).

White and Barents seas and at least the western part of the Kara Sea.

Outside the USSR, it is probably found in the adjoining regions of Norway.

4. Siberian ringed seal, *Ph. (P.) h. birulai* Smirnov, 1929.

Its size is large. The color of the hair coat is lighter than that of the Pomorsk ringed seal. The condylobasal length of the skull is 179-195 mm ($\bar{x} = 185.7$) (Ognev, 1935).

Seas of the eastern arctic sector: from the eastern part of the Kara Sea to the threshold of the Chukchi Sea.

Not reported outside the USSR.

5. Bering Sea ringed seal, *Ph. (P.) h. krascheninnikovi* Naumov and Smirnov, 1935.

It is of moderate size, smaller than the Siberian subspecies. Its color characteristics have not been determined. The condylobasal length of the skull is 152.8-189.5 mm; males average 174.2 mm and females 168.2 mm (Fedoseev, 1965b).

Bering Sea.

Outside the USSR, it has been sighted in American waters of the Bering Sea.

6. Okhotsk ringed seal, *Ph. (P.) h. ochotensis* Pallas, 1811 (syns. *gischiensis*, *nummularis*).

It is of small dimensions, the smallest form in the USSR waters. Color characteristics have not been established. The body length including the tail is 101-135 cm along the dorsal curvature; males average 117 cm and females 116 cm (Tauisk Bay; Fedoseev and Yablokov, 1965).

The condylobasal length of the skull is 152.2-176 mm (\bar{x} = 163) (S. Naumov and N. Smirnov, 1936).

Sea of Okhotsk.

Outside the USSR, found in the waters of Hokkaido.

* * *

The following subspecies are usually recognized in the waters outside the USSR: (1) *Ph. (P.) h. hispida* Schreb., 1775—western Atlantic Ocean including Greenland, Canadian waters up to the Beaufort Sea; (2) 179 *Ph. (P.) h. saimensis* Nordquist, 1899—Lake Saimaa in Finland; (3) *Ph. (P.) h. beaufortiana* Anderson, 1943—western polar Canada, Beaufort Sea; and (4) *Ph. (P.) h. soperi* Anderson, 1943—Baffin Island lakes.

The last two subspecies require thorough verification; they are sometimes placed (Scheffer, 1958) among the synonyms of *P. hispida hispida*. Judging from the latest data (Fedoseev and Nazarenko, 1970), no differences whatsoever could be identified between the populations inhabiting, on the one hand, the southeastern part of the Barents Sea and, on the other, the northern part of the Bering Sea. Evidently the entire arctic belt of Eurasia is inhabited by only one "Pomorsk-Siberian" subspecies or even the monotypical subspecies *Phoca hispida hispida* Schreber, 1779. In the latter case the rest of the forms of ringed seals indicated for our northern seas from the Barents to the Bering, i.e., the Pomorsk, Siberian, as well as the Bering subspecies, should be regarded as synonyms of the nominal form. (K.Ch.)

Biology

Population. Among the total population of seals in our waters, the ringed seal holds first place. A preliminary assessment of the total population in the USSR waters gives a figure of three million (Chapskii, 1966).⁵⁴ The majority, about 2.0-2.2 million, inhabit the polar sector from the eastern part of the Barents Sea to the Bering Strait.

The quantum of ringed seals inhabiting the Sea of Okhotsk, roughly calculated by applying the age-related structure analysis of animals caught at random, recognizing the relative proportion of the mothers (21%) and the proportion of annual births, etc., was placed at a maximum of 800,000 (Fedoseev, 1966b, c). Similar figures, i.e., 600,000 to 865,000 were arrived at in subsequent aerial surveys (Fedoseev, 1968). The

⁵⁴ The calculation is based on a quantitative assessment of the reserves of the ringed seal in the waters of the eastern part of the Canadian archipelago, where they are put at almost one million (McLaren, 1958) and extrapolating this value to the USSR range (with allowance for the varying habitation of the ringed seal in different sections of the range).

differences in the calculations are explained as due to error in the method of calculation (G.A. Fedoseev).

In the Bering Sea ringed seals are evidently fewer than in the Chukchi and East Siberian seas (Tikhomirov, 1966b). In 1964, aerovisual surveys estimated 12,000 ringed seals on ice floes in the western part of the Bering Sea (Shustov, 1969b).⁵⁵

From our present knowledge, it is impossible to establish the actual population of ringed seals in the Chukchi, East Siberian, and other arctic seas. Evidently in each of the arctic seas the reserves of ringed seals are extremely divergent. It can only be assumed that in the USSR part of the Chukchi Sea the ringed seal is more abundant than in the Bering Sea and less so in the Laptev than in the East Siberian Sea. Evidently the two latter seas are next to the Kara Sea in this respect. Possibly the Barents Sea has a higher population of ringed seals than the Kara Sea and evidently the White Sea also.

180 In the Sea of Okhotsk, as in the other seas, the ringed seal is very unevenly distributed. In April, during the breeding and lactation period, most of the animals localize mainly in three regions: the northwestern part of the sea (near the mainland coast from Tauisk Bay to Ayan), Shelikhov Gulf, and on the eastern coast of Sakhalin, including Terpeniya Bay. The bulk of the population is seen every year in the northwestern part of the sea. In the other regions (in Shelikhov Gulf and on Sakhalin), the population of the Okhotsk ringed seal varies significantly from year to year depending on the position of ice floes suitable for breeding. Thus in 1968, during the first 20 days of April, only 3,500 pups and 25,000 adults were counted (aero-visual survey) on ice floes and in the waters of Sakhalin; in the very next year, however, in the first ten days of the same month, there were 32,000 pups and 106,000 adults (Fedoseev, 1970). An animal density on ice floes during the pupping season of, on average, 1.5 animals per km² is not high.

Rookeries of molted animals are found in May when intense thermal and dynamic break-up of the ice floes occurs. The animals actively migrate to those regions where the ice floes remain intact longer. Large collections of the molted Okhotsk ringed seal are usually noticed in the region of Eirineisk Bay and in the Sea of Okhotsk, Khanyangda-Ayan, on the Shantarsk Islands, in Sakhalin and Shelikhov gulfs, and on the

⁵⁵ This figure cannot, in fact, reflect the actual size of the population (only the animals seen on ice floes were taken into account). The actual population in our part of the Bering Sea is higher. The figure indicated constitutes only a third, until recently, of the total annual catch of the ringed seal on the coasts of the entire Chukchi Peninsula (see p. 257) and only double the number of ringed seals caught in 1960 on the southern and western coasts of the Chukchi.

northeastern coast of Sakhalin. This seal is encountered in small numbers on the northeastern coasts of Kamchatka. Stray ringed seals are encountered in the northwesternmost part of the sea adjoining La Perouse Strait (G.A. Fedoseev).

In the Bering Sea almost all the animals are confined year round to the coastal belt extending northeast of Karaginsk Island to the Gulf of Anadyr. The ringed seal is evidently concentrated in large numbers in the Gulf of Anadyr. On the southern and eastern coasts of the Chukchi Peninsula, the maximum concentrations during reproduction and molt are noticed in Krest Bay, in the region of Rudder Spit, and all along the coast of the Bering Strait to Cape Dezhnev.

In the Chukchi Sea, the sections close to Cape Serdtse-Kamen', the region of Kolyuchin Bay, and slightly northwest of Kolyuchin Island, are prominent in abundance of the ringed seal (Fedoseev, 1965c). In the East Siberian Sea, the ringed seal is more numerous, even abundant in summer on the Medvezhii Islands and generally in the eastern part of the sea; on the contrary, on the Novosibirsk Islands it is rare (Mikhel', 1937). The southwestern part (region of Begichev Island-Nordvik Bay of the Laptev Sea), as far as can be judged from the scant data (Koshkin, 1937; L. Popov, 1941*), is quite rich in the ringed seal.

In the Kara Sea the ringed seal is more numerous on the northwestern coast of Yamal, in the region of White Island, and the northern portion of Gulf of Ob, on Dixon Island, and in the adjoining sections of Yenisey Bay, in the region of the Pyasine estuary, Minin Sea cliffs, and on Cape Sterlegov. Significant congregations are seen in the midpart of the Novaya Zemlya strip of the sea, especially from Matochkin Shar to the Pakhtusov Islands. At almost all these places the ringed seal is not a permanent resident; it is seen in spring and sometimes in summer or, on the contrary, abandons these regions in summer and autumn.

The chief sites of concentration of the Barents Sea ringed seal are the southeastern coastal regions of the sea in which the largest number of arrivals is seen in the autumn-winter months: the regions of Kambal'nitsa and the adjoining islands (northeastern coast of Kanin), some sections of Cheshsk Bay, regions of Sengeisk Island (with the strait), Kolokol'kovsk Bay, Pechora Bay, Varandei Island, Khaipudyrsk Bay, western "mouth" of Yugorsk Shar, southeastern coast of Kolguev Island, rock cliff in the southern part of Novaya Zemlya including the region of Mezhdusharsk Island, Belush'ei Bay, and others.

The population and regions of maximum concentration of ringed seals in the White Sea are as yet not adequately known.

In the USSR territorial waters of the Baltic, based on aero-visual observations, about 12,000 ringed seals were estimated (V.A. Zheglov;

181 Zheglov and Chapskii, 1972*). Of these, 8,000 were in the USSR territorial waters of the Gulf of Finland and about 4,000 in the Gulf of Riga. The total population of the Baltic ringed seal at present is estimated at roughly 50,000 (V.A. Zheglov). In winter the seals stray far from the coasts and are confined mainly to deep-water zones; depending on the formation and thawing of ice floes, these animals move into shallow-water sections in the environs of islands (V.A. Zheglov).

The Lake Ladoga population is less than in the past (Chapskii, 1932*; and others); it probably does not exceed 5,000-6,000 (A.A. Antonyuk).

Habitat. As the ringed seal belongs to the group of pagophilic seals (associated with ice floes), it usually inhabits those water bodies which are icebound, at least in winter. It selects for breeding predominantly the coastal, stationary ice floes. Only the Okhotsk ringed seal deviates from this rule and probably the Chukchi ringed seal at places. As a result of intense tidal currents in the Sea of Okhotsk, stable shore ice is not formed and the Okhotsk ringed seal is forced to use the broken-up ice floes drifting in the relative proximity of the coast for breeding and molt. Further, this seal undergoes parturition at some distance from the edge turned toward the coast, selecting fairly firm, somewhat piled-up ice floes. Any fairly firm ice floe with air holes in the vicinity serves as a whelping site. In most cases, pups lie in the open and not under a snow cover (N. Smirnov, 1911; Tikhomirov, 1961; Fedoseev, 1964b*, 1965; and others).

In all the other regions the ringed seal is confined during the breeding season to shore ice or coastal ice floes concealed under a snow cover from the gaze of passersby. The pups are delivered in snow caves on the ice floe, near an air hole, or in hollows formed among heaps of broken-up ice floes.

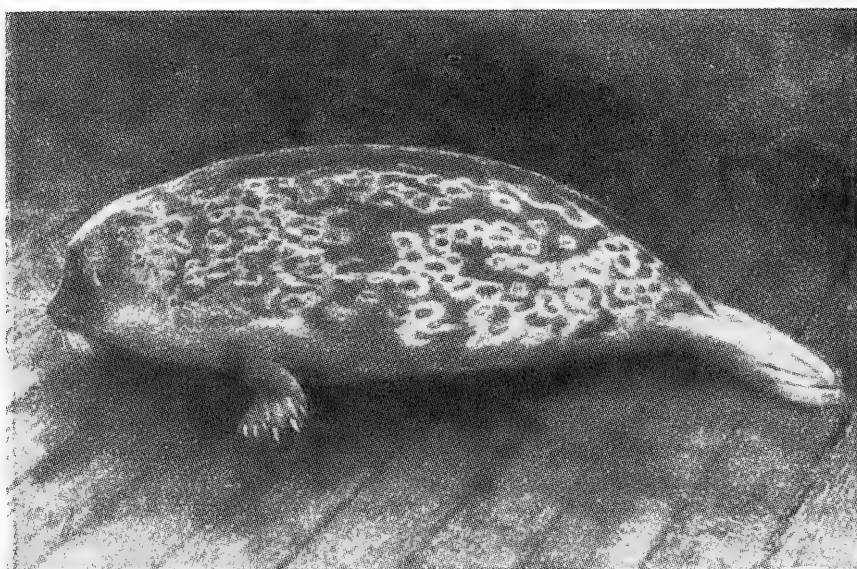
182 The young animals (Fig. 114) not participating in reproduction (and also evidently even a part of the adult males) remain beyond the range of stationary shore ice in nearby sections of broken-up and drifting ice floes. The arctic ringed seal remains even much later, in the period of molt, in air holes mainly on the same coastal stationary ice floes that are breaking up with time and warmth. In addition to pups of the current year, young animals also gather here and after lactation and shedding of the embryonic pelage depart from the shore ice. During this period the ringed seal greatly enjoys resting on the ice floes preserved for a long time along the highly rugged coasts and in the straits between islands. Such, for example, are the southern coasts of Novaya Zemlya, the coastline of the Bering Strait, and many other parts of the range. Nevertheless, ringed seals do not avoid even the shallow sections with a fairly even coastline, such as the Yamalsk shallow-water zone in particular or the

northern coastal strip of the Chukchi Peninsula. Naturally, under such conditions the ringed seal colonizes far away from the coast, beyond the limits of compact ice masses.

In the Sea of Okhotsk, however, during molt the ringed seals rest once again on small, preferably isolated ice floes. At this time they evince no interest whatsoever in site selection and can be seen resting on clean or soiled, hummocky or smooth ice floes; sometimes they are seen even on top of a hummock (Pikharev, 1941).

Beach rookeries are not very typical of this species, especially in the arctic zones and in the Far East.

The ringed seal does not rest often in summer or autumn on the coast in the western parts of the Soviet arctic and subarctic sections of the range. Its rookeries are known on dried-up spits in the White Sea Inlet (e.g., on Lidtko Spits, etc.), in the estuarine zone of the Eastern Kambal'nitsa (along the northeastern side of the Kanin), and in the estuaries of some Murman rivers, including Voron'ei. Further, ringed seals rest on rock ridges, "ludas," and "kirevyadi" at several places on the Ladoga coast, and at places on the coasts of the Gulf of Finland and Gulf of Riga in the Baltic Sea. At places they enter the rivers but do not usually ascend far upstream.



181 Fig. 114. Immature ringed seal, *Phoca hispida ochotensis*, Bering Sea, June, 1964
(photograph by G.M. Kosygin).

Food. The ringed seal feeds on fish and crustaceans; other animal groups (mollusks, worms, cephalopods, etc.) are consumed only very rarely and are not at all characteristic of its diet. It feeds mainly in the upper water layers on animals that are available en masse. Benthic food is resorted to only in shallow places.⁵⁶ The quantity-wise ratio of fish and invertebrates consumed varies in different seasons according to the periodic concentration of a given food type. In the autumn-winter months the importance of fish increases noticeably; in some regions, e.g., Novaya Zemlya, with the en masse arrival of the polar cod, fish food can be highly predominant and be even the mainstay in its diet.

In the spring-summer months, contrarily, the ringed seal feeds mainly (sometimes at places even exclusively) on the various forms of crustaceans abundantly available. Thus in the Kara and Barents seas ringed seals were caught with their stomach packed with either amphipods (*Themisto* sp.) or mysids (*Mysis oculata*).

Like other seals, the ringed seal feeds sometimes more intensively and sometimes less so in different seasons. The main season of its feeding covers the middle of summer, the entire autumn, and early winter. In spring, i.e., at the time of mating, feeding is evidently poor. It is less intensive in the protracted period of molt because of the long residence of the animals on ice floes. Nevertheless, there is no prolonged total abstinence from food by this species.

In the Sea of Okhotsk, during spring (from February through June) the ringed seal feeds mainly on the black-eye euphausiid (*Thysanoessa raschii*) while the amphipods (mainly genera *Gammarus*, *Themisto*, and *Anonyx*), shrimps (genera *Pasiphaea*, *Pandalus*, and *Spirontocaris*), mysids (*Mysis*), and partly sea slaters (*Mesidothea* and *Idothea*) play a lesser
183 though significant role. Fishes such as pollock, pond smelt, navaga, and more rarely herring (S. Naumov, 1941) are consumed in these months in a comparatively small quantity (roughly at 10% by weight) (Fedoseev, 1965e) and represent over 35% of the number of species identified (Pikharev, 1946).

In summer, at the end of molt, the ringed seal feeds intensively far away from the coasts, evidently mainly on the planktonic organisms and primarily on the black-eye, which clearly predominates; it also thrives apparently on the schools of capelin which are attracted to the black-eye and other planktonic species (Fedoseev, 1965e).

⁵⁶ The depth of submergence can sometimes reach 60 m or more based on the fact that the food of the ringed seal often includes the common sand eel (*Ammodytes hexapterus*) which prefers to settle and spawn at such depths.

In autumn and early winter the ringed seal feeds more on fishes (navaga, smelt, small herring, sometimes goby, sand eel, etc.). Since it quite often transgresses even into rivers, especially in Kamchatka, the ringed seal is assumed to consume salmon also (Lun', 1936; Freiman, 1936). Although precise data are not available on this subject, the alleged consumption of salmon by the Okhotsk ringed seal is erroneous. From among the crustaceans, it consumes at this time predominantly shrimps and amphipods, fewer euphausiids, and least of all, mysids (Fedoseev, 1965e).

The food of the ringed seal in the Bering Sea has not been investigated fully. In the transition period of spring and summer it feeds almost equally on fishes (mostly the polar cod) and crustaceans (shrimps including amphipods, and more rarely on mysids and black-eye). At this time on the USSR coasts of the Chukchi Sea the ringed seal feeds more on amphipods and shrimps and less on fishes (mainly on navaga, and sometimes flounder) (Fedoseev, 1965c). In winter, however, the ringed seal in the Chukchi Sea survives almost exclusively on fishes, mainly the polar cod (Johnson, Fiscus *et al.*, 1966).

In the western seas of the Soviet arctic (the Barents, including Pechora, and the Kara) the ringed seal consumes the very same two groups of abundantly available foods: fishes and crustaceans. Polar cod plays an exceptional role among the former and serves as the main food in the autumn-winter period when huge schools of this small fish arrive at the coastal regions to spawn. Seasonal concentrations of polar cod attract the arrival and at places significant concentrations of the ringed seal in the autumn-winter period on the coasts not only of Novaya Zemlya and Vaigach, but also Timansk tundra, Cheshsk Bay, White and Kara seas. In this manner, but on a smaller scale, concentrations of the ringed seal are also stimulated by other schools of fish, e.g., the arrival of navaga in the Pechora Sea and other regions. At the beginning of this century, herring was abundantly found in the stomach of ringed seals caught on the Murman coasts (Soldatov, 1902) when this fish was available there en masse; the ringed seal also consumed capelin on these coasts. It was assumed that the ringed seal noticed in the river estuaries of the Murman coasts and transgressing fairly long distances upstream could even thrive on salmon (N. Smirnov, 1903) but not accurate data are available (see p. 257). In the Gulf of Ob ringed seals falling in fish traps ate omul but this fish was not found in the stomach of seals caught in the open. Young char were sometimes found in the stomach of the Novaya Zemlya ringed seal. In fact, in the spring of 1904, the remains of a salmon were found in a salmon net (Breitfus, 1908). There is now hardly any doubt that the real culprit is the common seal. Yet the view that the ringed

seal preys on salmon persists here and there. This is evidently promoted by the fact that the ringed seal can actually live at some places on the very large fishes caught in nets; otherwise it could not have survived. Whatever the reason, it is still firmly believed that "the whitefish plays a significant role in the food of the ringed seal" (Kirpichnikov, 1937) and the small population of the ringed seal in the Yenisey-Pyasinsk region of the Kara Sea is castigated for the poor arrival of the omul (*ibid.*), or that the ringed seal in the western seas of the Soviet arctic consumes salmon and omul along with other fishes (Golenchenko, 1961).

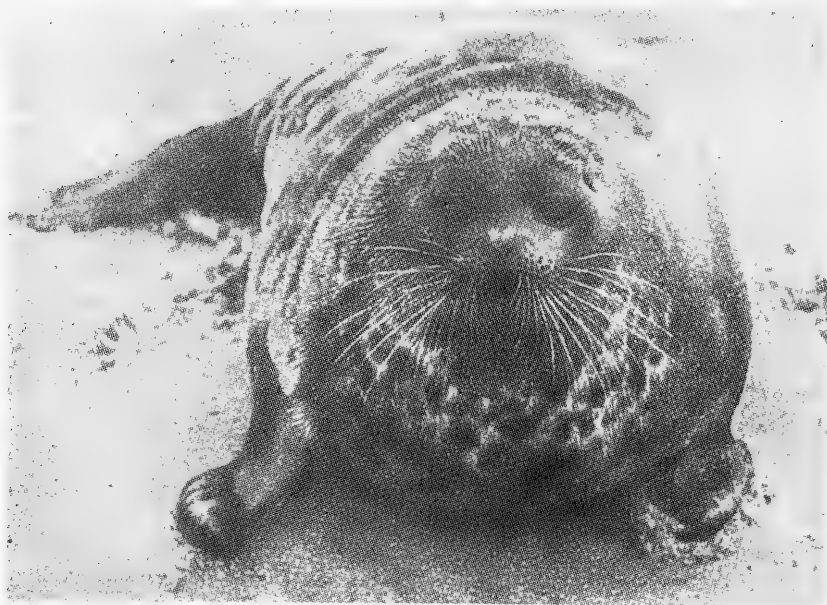
In addition to fish, even in the west these seals consume amphipods (mainly *Euthemisto* sp., *Gammarus* sp., and *Gammarocanthus loricatus* and *Anonyx nugax*), a mysid (*Mysis oculata*), a euphausiid—black-eye (*Thysanoessa inermis*), and shrimps (*Eualus gaimardi*).

184 The food of the Baltic ringed seal has scarcely been studied in our territorial waters. Presumably this seal feeds on fishes and crustaceans on the Estonian coasts too but crustaceans play a minor role and are consumed mainly in the winter and spring; Baltic herring and sprat take first place among fishes; other fishes consumed include cod, eel, omul, and even pike-perch (Aul, Ling, and Paaver, 1957). According to other data, the Baltic ringed seal consumes mainly sprat and also goby, snailfish, and amphipods; in the spring, however, it feeds mainly on the sea slater (Schubart, 1929). Recent investigations showed that, in the Baltic Sea, the ringed seal feeds mainly on the slater, goby, eelpout, small Baltic herring, smelt, sprat, and stickleback (V.A. Zheglov). Large fishes are evidently inaccessible to the ringed seal and it can only steal them from fishing nets.

In Lake Ladoga the ringed seal feeds for the most part on smelt, ruff, and small vendace. The stomach of this seal also contained stickleback and small crustaceans (A.S. Sokolov, 1958; S.M. Sorokin). The view that the Ladoga ringed seal "feeds on whitefish, char, vendace, and other fishes" (A. Smirnov, 1961*), here too is evidently based on the instances of this seal stealing these fishes from nets.

Home range. Although ringed seals are usually regarded as settlers, their population is not confined to any one section of the sea year round. They migrate (see "Seasonal Migrations and Transgressions") with changing ice, food, and other conditions. It is therefore practically impossible to establish the definite boundaries and sizes of expanses occupied by one single animal or even the population as a whole.

The mothers exhibit the most distinct stationary distribution (excluding the Okhotsk ringed seals) and that, too, in the winter-spring period when the gestating and whelped female is confined to a single site selected by her for its suitability for pups to be born or already



184 Fig. 115. Ringed seal on a sandy shoal. White Sea, Severnye Koshki, September 20, 1970 (photograph by A.G. Beloborodov).

185 birthed. Such animals are scattered several hundred meters apart. The density of their disposition depends on the size of the population, extent of ruggedness of the coastline and the nature of the coast in general, the depth of the coastal zone, ice conditions, and so on. Juveniles of both sexes and even adult males are confined beyond the limits of the stationary shore ice, along its edge, and in the zone of broken drifting ice floes with open water pools. The degree of their concentration is much greater but yet variable under the influence of the above factors, mainly food conditions.

Hideouts and shelters. Ringed seals, like many other true seals, make air holes in the ice floe through which they crawl out of the water for respiration. The mechanism of making such holes is not known with certainty but it may be assumed that initially, when the crust of the ice floe is not yet very thick, the animal pierces it with its head by diving in the same manner as does the Greenland seal. The Baltic ringed seal can pierce an ice crust up to 2-2.5 cm thick in this manner (V.A. Zheglov). Subsequently, these holes are kept open by repeated use for respiration and later for crawling out of the water when the ice is thick. It is possible that the walls of the hole are worked up with the claws also

(N.A. Smirnov, 1927; Kirpichnikov, 1937); in any case, the claws of the ringed seal are powerful enough for this purpose.

The ice around the air hole builds up gradually and, when it is used exclusively for respiration, a semispherical arch is formed above the opening over the course of time, in which only the head or even only the tip of the snout protrudes (and hence the hole is not large). The arch is formed by snow built up from inside as a result of alternate thawing by the exhaled warm air and possibly the water spray freezing during the intervals in respiration. At the center of the arch, i.e., the dome, there is usually a small hole but it can altogether be concealed under the snow and wholly imperceptible from outside.⁵⁷ The coastal people call such "air holes".

There are many variations of the above-described typical air hole: it can be hidden in the hummocks, under a hanging ice floe, pressed out as a result of compression on the surface, in a niche formed under a pile of ice floes, in a fresh fissure, and so on. It is not quite clear whether the animal works on such a conical opening and, if so, in what manner. Probably, from time to time, the ringed seal has to enlarge it, working on it not only with the claws but also with its teeth.

Such openings quite often serve two functions: for respiration and egress from the water. In such cases they are considerably wider and less sharply narrowed upward, with a diameter of 30-40 cm or more on the surface of the ice floe. They are made initially like air holes and then, when the ice is quite firm to support the animal, are used for crawling onto the ice repeatedly. Due to constant use, such holes are not sealed by the ice nor are they highly frozen from inside.

Snowdrifts and the location of air holes promote this process. Although the holes are made under extremely diverse conditions, they are mainly concealed. When the hole is made by a gestating female, she often selects a section of the ice cover damaged by a fissure followed by compression, causing further opening up of the ice floe and the piling up of broken lumps. In such places there are open water pools which are rapidly closed by young ice along with randomly disposed ice blocks with niches and voids between them. Sometimes the ice floes invert and pile up one over the other in such a way that they form a typical roof with a pointed peak rising above the edge of the young ice floe. Ringed seals are particularly drawn to such natural hideouts for whelping.

Quite frequently, the ringed seal gives birth to pups in special lairs or holes made in snowdrifts among hummocks, around an ice floe elevated during compression, and at the base of drifting ice floes. Such holes are

⁵⁷ Air holes can also be concealed under a snow cover as a result of drifting snow.

also encountered directly in deep snow at almost a level surface. Such a lair can be detected only with the help of a dog. No one has ever seen how a ringed seal constructs its "nest". It is perhaps not very difficult in loose snow. It probably makes a hole in the snow, partly using all its physical might and partly by shaping it with its fore-flippers. Moreover, the heat radiated by the animal's body and its respiration somewhat thaw the snow and it evaporates. Further, the arch from inside the lair is sometimes lined with snow, which increases its strength. The roof of many such snow lairs found in southwestern Baffin Land could only be broken by applying force and after repeated trampling (McLaren, 1958).

The snow lairs made in the Kara Sea are usually longitudinal, about 170-185 cm long and 60-70 cm in height; they extend sideways from an air hole whose diameter varies from 34-45 cm. Sometimes there is a passage in the snow from the air hole into the snow chamber. The same animal can usually make more than one air hole which is used by other animals also. Only a single lair is usually built although according to some workers (A.N. Tyulin), there can be spare ones. Judging from all the information, mainly, if not exclusively, adult females make lairs, and essentially for protecting their pups.

Among the Chukchi ringed seals, the snow lairs are much larger in size with an area of 3 to 7.5 m² and 2-3 air holes. In winter such "caves" can afford protection to several animals. Individual stray air holes (without lairs), opening outward, are disposed quite close to the lair. The upper diameter of the ice holes opening into the lair varies from 80 to 120 cm while the thickness of the ice in which it is made can be 95 to 110 cm and the height of the snow cover 85 to 125 cm (Fedoseev, 1965c).

Daily activity and behavior. Precise data on this aspect are not available. Visual observations in different regions, different seasons, and in different environments provide no categorical answer. In the summer-autumn season the ringed seals regularly remain in water, feed there, move from place to place, rest, and sleep at any time of the day. In spring and early summer they can be seen resting by the side of an air hole or pool and sleeping much of the time for days on end, especially in good weather.

Judging from the fact that ringed seals are trapped more often at night in the nets set for them (and even in fishing gear), it can be concluded that these animals are also active at night. Evidently even in the season of intensive feeding, they sleep several times during the day, i.e., after every full meal.

The more active spring behavior among the Okhotsk ringed seals disposed on broken drifting ice floes is somewhat different. "Rookeries

are always buzzing with activity, with the seals diving into the water and crawling onto the ice time and again" (Fedoseev, 1965f).

Seasonal migrations and transgressions. These aspects are relatively less manifest among ringed seals and have not yet been fully studied. These are largely passive activities, resulting from seasonal movements of the ice floes with which this seal is associated almost from the beginning of the arctic summer.

In the Sea of Okhotsk, corresponding to the predominantly anti-clockwise flows, the bulk of the Okhotsk ringed seals move in the spring from the northeastern regions of the sea (from the Penzhinsk, Gizhiginsk bays and Shelikhov Gulf) to the southwest (see Fig. 112). This was hinted at even in the early 1930s (Razumovskii, 1933). There were contrary opinions too (S. Naumov, 1941). From the end of March when the whelping season commences and the animals spend much of their time on the ice, their maximum concentrations are seen in the region of Tauisk Bay, on the threshold of Shelikhov Gulf, and in its southwestern part. By May, the animals extend to the expanse in the Khanyangda-Okhotsk zone; by June, they move into the Ayan region in the western part of the Shantar Sea; still later, from June end through July end, they are concentrated in the southwest from Shantarsk Bay to Sakhalin Gulf and in the regions east of Sakhalin. Such is the usual passive drift of the lactating and molting ringed seals and those simply "enjoying a sun bath" under the influence of snowdrifts (Nikulin, 1937; Pikharev, 1940*; Tikhomirov, 1961; Fedoseev, 1965f; and others).

Some basis for the possible active migration of the Okhotsk ringed seal was reported very recently. While observing the concentrations of these seals in the western regions of the Sea of Okhotsk from a plane, it was noted that, in spite of powerful, stormy western and northwestern winds driving the ice floes toward Kamchatka, the Okhotsk ringed seals did not move with them; they were sighted a few days later en masse in the northern and western parts of the sea (G.A. Fedoseev).

At the end of the season, the ice floes become very thin and the ringed seals abandon them and begin to feed voraciously. Their movements now are associated with the migrations of schools of fish and with the distribution of planktonic and nektonic crustaceans. With time, the number of ringed seals in the western regions of the sea decreases noticeably and, concomitantly, massive and active movements of herds of ringed seals are noticed in the water (Freiman, 1936) in a reverse direction; i.e., to the northeast. The population of the ringed seal again increases sharply from September in the extensive coastal expanse in the region from Tauisk to Shelikhov bays where the bulk of the Okhotsk ringed seals spend the winter. However, such a large cycle of migrations

does not evidently occur invariably (Fedoseev and Yablokov, 1965); even in the years when migrations assume large dimensions, a part of the population remains there leading a semisettled, semiwandering way of life all along the coastal belt from Penzhinsk Bay to Sakhalin. In any case, in winter and spring the Okhotsk ringed seal leads a settled mode of life (Fedoseev, 1971).

Migrations of one type or the other are typical of other populations too. Most of the ringed seals abandon the Bering Sea and even more so the Chukchi Sea with the spring-summer break-up of the coastal ice floes and their drifting. Deep in autumn, they return again to the northern coasts of the Chukchi with the appearance of fresh ice floes (Arsen'ev, 1935). In the Bering Sea the rest of the population is scattered on the beaches; many animals transgress into the lower courses of the rivers, including the Anadyr, and sometimes ascend to a considerable distance (Gondatti, 1897; Portenko, 1941). Sometimes the ringed seals are unsuccessful in entering the sea before the rivers freeze and, in such cases (evidently tragic), once again seek their way to the sea on ice floes and even on land. Some cases of simply unbelievable finds of ringed seals in hilly and wooded locations, where they strayed while looking for the sea, have been reported (Portenko, 1941; Ostroumov, 1960; and others). Similar cases have been reported in the west too (Vrublevskii, 1959; Chentsov, 1959; Vishnyakov, 1961; and others).

It is quite possible that the ringed seals from the southern coasts of the Chukchi move north through the Bering Strait in summer.

The ringed seals of the western seas of the Soviet arctic perform fairly regular migrations. Novaya Zemlya hunters distinguished even in the 1930s the "arriving" and local ("well-settled") ringed seals. With the onset of summer and the thawing of ice floes, the former abandon the coastal strip on the southern part of Novaya Zemlya and migrate through the Kara Strait into the Kara Sea; with the onset of autumn, they again return by the same route. The autumn-winter arrivals of ringed seals on the coasts of Novaya Zemlya, Timansk tundra of Kanin Peninsula, Kolguev and Vaigach islands, and other regions of the Pechora Sea and into the White Sea in the north as well as the Kara Sea, are associated
188 mainly with the en masse arrivals of spawning polar cods and at places with the similar arrivals of smelt and navaga.

The Baltic ringed seals also perform local migrations. Thus the population reproducing in Riga Bay arrives there in autumn and, with the thawing of ice floes in spring, goes elsewhere into the open sea for the summer (Leis, 1960).

Some periodic variations are noticed even in the distribution of the Ladoga ringed seal. From time to time it gathers in one or the other

part of the lake, these movements sometimes being associated with the migrations of vendace or even whitefish and char (A. Smirnov, 1954).

Reproduction. The mating period among ringed seals, as among other pagophilic seals, falls in the spring and sets in evidently at the end (or in the second half) of the lactating period.⁵⁸ In the absence of direct observations, the mating season has to be judged from the state of the gonads and other indirect features. Empty seminiferous tubules of large diameter at the end of May and, contrarily, active spermatogenesis from early February through early May, and some other data suggest that the mating period of ringed seals in the Barents and Kara seas extends from April end to at least the first 20 days of May (Chapskii, 1940). The intense growth of follicles commences immediately after whelping, simultaneous with the resorption of the corpus luteum of the preceding gestation. An increase in the total weight of the ovaries is also associated with this feature. Similar data suggest that the mating period among the Okhotsk ringed seals too falls in nearly the same period, i.e., in the second half of April to the first half of May (Fedoseev, 1964a, b, 1965b; Tikhomirov, 1966d*). The mating of the Bering ringed seals evidently concludes in May (sperm were not detected in the epididymis of the males in June; Fedoseev, 1965c). According to other information (Razumovskii, 1933), the Chukchi ringed seal presumably mates in March and April.

In the Baltics, corresponding to the prolonged whelping, mating occurs mainly in April but could occur even in March, ceasing by April end (Aul, Ling, and Paaver, 1957; Leis, 1960).

The mating season among the arctic ringed seals evidently proceeds without serious conflicts between the males; this is due to the scattering of the animals which do not form herds either in early spring, at its end or in early summer. No traces of injury whatsoever, that could be attributed to fights between competitors, have been noticed on the skin of males. Nevertheless, due to the limited population of males and reproducing females, fights do arise at some places. For example, in Riga Bay the male resists any intruder attempting to approach a chosen female by grasping his flipper (Leis, 1960).

Males capable of reproducing are usually not younger than six years and most of them become productive for the first time only at seven years of age.

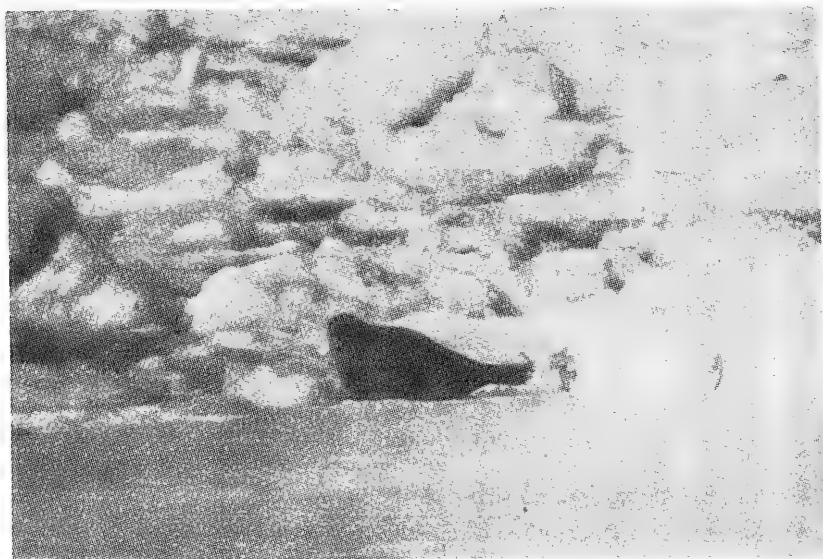
Such a late maturation was reported among the eastern Canadian and Far Eastern populations (McLaren, 1958; Fedoseev, 1965b;

⁵⁸ An earlier view that the Okhotsk ringed seal mates in the second half of July and in August after molting (Sleptsov, 1943) is based on an error arising from ignoring the lag in the implantation of the blastocyst.

Tikhomirov, 1966d*). It has been assumed that about 20% of the males of the Okhotsk ringed seal mate for the first time even in the 8th year (Fedoseev, 1964).

Maturation among females sets in somewhat earlier. They undergo parturition at the earliest in the 5th year according to some authors (Fedoseev, 1964a, b; Tikhomirov, 1966) and according to others (McLaren, 1958), in the 6th year. However, the percentage of females maturing early is not high. Quite a few females give birth in the 6th or 7th year. A small number produce the first pup in the 8th year. The
189 youngest mothers among the Barents ringed seals are 6 years old but their number, about 3%, is very small (Nazarenko, 1965).

Embryonic growth is impeded right at the initial stage of fission of the fertilized egg cell [delayed implantation]. The duration of this period among the Barents and Kara ringed seals was originally regarded to be about two months (Chapskii, 1940). It later became clear that the implantation of the blastocyst among the Canadian ringed seals occurs roughly 3.5 months after fertilization (McLaren, 1958). The duration of the latent period among the Okhotsk ringed seals is 2.5-3 months (Fedoseev, 1965b).



189 Fig. 116. Ringed seal on ice floes. Barents Sea, April, 1967 (photograph by V.A. Potelov).

Even in the period of peak reproductive activity, not all ringed seals undergo parturition every year. In the Canadian population the average percentage of barren females is 5-10 (McLaren, 1958, 1960) although according to recent calculations, it was assumed that only one-half of the eligible population gave birth to pups (McLaren, 1967*). A fairly significant percentage of barren animals was reported among the Far Eastern ringed seals (20% on average among the Okhotsk ringed seals; Fedoseev, 1964c*)⁵⁹ and even more among the western arctic ringed seals, of which 37.5% of the adults were without pups (Nazarenko, 1965); V.A. Potelov puts this figure at as high as 50%.

Early spring is the period of whelping but it is quite protracted even in a given region in the USSR part of the range as a whole, extending for at least two months. In the Baltic basin, on the Estonian coasts and more northwards, the ringed seals whelp mainly at February end to early (more rarely end of) March (Lönnberg, 1899; Nordquist, 1899; Schubart, 1929; Freund, 1933; Ropelewski, 1952; Aul, Ling, and Paaver, 1957), and in Lake Ladoga in early March.

In the White Sea, on Murman, southeastern parts of the Barents Sea (close to the Novaya Zemlya coasts, in the southeastern parts of the Pechora Sea, in Cheshsk Bay, close to Timansk coast, and in Yugorsk Shar), the ringed seal whelps near about the same time, mainly from the middle or end of March through the middle of April, and sometimes even later (N. Smirnov, 1903; Knipovich, 1907; Ognev, 1935; A.N. Dubrovskii; M.I. Vladimirskaia; Yu.I. Nazarenko; V.A. Potelov; and others). In the Kara Sea this seal whelps evidently somewhat later, mainly in April, though the data on this are contradictory and limited (Kirpichnikov, 1937; Kovalev, 1938; Tyulin, 1938).

In the northern part of the Sea of Okhotsk, in the region of Tauisk Bay, pups arrive from March to mid-April (Tikhomirov, 1961), mainly in the second half of March and the first half of April (Fedoseev, 1964b*). About the same time, ringed seals on the coasts of the Chukchi Peninsula also undergo parturition (Razumovskii, 1933; Fedoseev, 1965c). In Tatar Strait, whelping extends from mid-February to probably mid-May (Dorofeev, 1936; S. Naumov, 1941; Yu.A. Salmin).

Growth, development, and molt. Unlike most other species of seals, the initial postnatal period has not been adequately studied with the exception of the Okhotsk population. This is explained by the fact that birth, lactation, and shedding of the embryonal pelage are all concealed in the snow cover from the first appearance of the newborn almost until

⁵⁹ According to Tikhomirov (1970), however, barren seals in the Far East constituted only about 7%.

it becomes self-supporting. Only in the Sea of Okhotsk and in Tatar Strait are pups born in the open; but even under these conditions, the pup tends to remain among the hummocked ice or the icy ledges to protect itself from the wind. Having selected such a site, it does not leave it for long without purpose; a troughlike depression even forms in the ice floe due to the prolonged resting of the pup at the same place (Pikharev, 1941).

The embryonic coat of the newborn is creamy-white with a faintly discernible greenish or grayish tone in the first few days. In some populations (especially in the case of the Ladoga ringed seals), it is quite often covered with a smoky-brown bloom dorsally. The embryonic coat is almost as long and dense as in the newborn of other proximate species but is inferior in fineness, abundance, and luster (Fig. 117).

- 191 How long the pup sports the embryonic coat has yet to be accurately established but evidently it is longer than ten days. Since the pups of the Okhotsk ringed seal are seen with an embryonic coat mainly from the second half of March through the first half of April (Fedoseev, 1964b*) and at the end of the first five days of May have only just begun to molt (Pikharev, 1941), the firm hair coat apparently endures for at least two weeks.

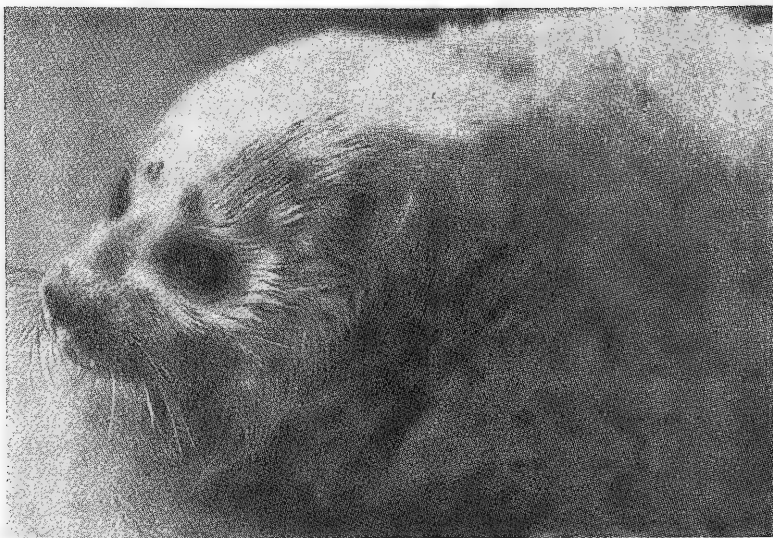


Fig. 117. Head of a ringed seal pup that has not shed its embryonic hair coat. Bering Sea, June, 1964 (photograph by G.M. Kosygin).

The duration of molting of pups in the course of their suckling evidently conforms to a common pattern. Among the normally grown animals, molt commences from the snout while the bases of the fore and hind flippers and the tail evidently molt later; the embryonic coat lasts longest on the body flanks and also on the belly. Even before the weakening of the embryonic coat, the growth of the hair characteristic of the subsequent stages commences.

The body length of the newborn varies from 55 to 65 cm; more often about 60 cm (*Lc*, i.e., along the body surface up to tip of tail); weight varies from 3.5 to 4.0 kg.

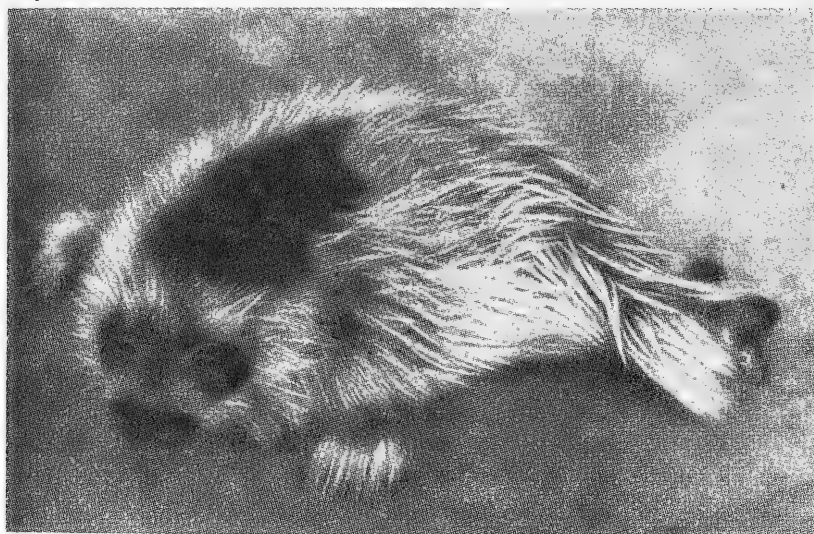
Lactation continues for not less than a month, evidently until the pup has completely molted. The mammary glands of the Okhotsk ringed seal function until mid-May; until this period, the intestines of the pups contain no food other than milk (Fedoseev, 1964b*). During the suckling period pups of the Okhotsk ringed seal grow to 64-72 cm (average up to 67 cm) and almost double their initial weight (raised to 6-9 kg, average up to 7.5 kg). In the last seven months, by November, they add another 10 cm (average) in length and roughly 4.5 kg in weight, thus reaching 72-84 cm in length (*Lc*) (average 78 cm) and 10-14 kg in weight (average 12 kg) (Fedoseev, 1964b*). Similar figures have also been recorded for the pups of the Bering ringed seal (Fedoseev, 1965c).

The autumn yearlings of the Barents ringed seal are larger, with a body length (*Lc*) varying from 74 to 103 cm, average 91 cm (the data are not sufficiently representative) (Chapskii, 1940).

Under unfavorable growth conditions, when the pups lose suckling mothers or become ill for example, they remain underfed but nevertheless do not die; they do not grow to the size normal for their age and remain dwarfs. Such animals are encountered time and again on ice floes in the White and Barents seas. The coastal people call such starved animals "kavadei" or "telesai" (Fig. 118).

Further growth of the young before the onset of maturation is low, as can be seen from the following changes in average body length (*Lc*) and average weight of the Okhotsk ringed seal:

	Length (cm)	Weight (kg)
One-year-olds	84	14
Two-year-olds	92	19
Three-year-olds	98	24
Four-year-olds	102	27
Five-year-olds	106	29.5
Six-year-olds	110	32
Seven-year-olds	113	34.5



192 Fig. 118. Underfed pup ("kavadei" or starved) of a ringed seal in a state of delayed molt. White Sea, April 12, 1967 (photograph by V.A. Potelov).

Growth and weight continue to rise in subsequent years also but stabilize from 10 years of age at an average length of 119-122 cm and weight of 40-44 kg (Fedoseev, 1964b*).

The period of molt among juveniles, commencing from yearlings, and among adults is highly protracted. In the western arctic seas of the Old World, molting individuals are encountered even in May but June and July represent the more normal molting period in the Barents and Kara seas; the animals lagging behind complete molting as late as August. On the western side of Novaya Zemlya, molting individuals constitute a scattered herd far removed from each other on the smooth ice floes among the shore ice.

- 192 In the Sea of Okhotsk ringed seals molt on drifting ice floes in very dense groups from April end through mid-July. The adult males begin to molt two to three weeks earlier than the gestating females and hence molting of the latter is correspondingly more extended. Unmolted juveniles are encountered not only in August, but presumably even in September (Fedoseev, 1965f), although molting in the majority of these seals ceases in the first half of July under normal conditions (S. Naumov, 1941; Tikhomirov, 1961).

Enemies, diseases, parasites, mortality, and competitors. In the arctic zone the polar bear continues to date to be the number one enemy of the

ringed seal, even through the predator's population in the twentieth century has sharply decreased everywhere, especially in the western regions, including those along the coasts of the southern island of Novaya Zemlya and also in most of the regions of the Kara Sea. This predator of the ringed seal has been exterminated almost wholly in the southeastern part of the Barents Sea, in the southwestern part of the Kara Sea, and in its Yamal-Obsh-Yenisey region. At places where the polar bear still continues to exist, it has survived mainly on the ringed seal. The Greenland shark (*Somniosus microcephalus*) is the second enemy but mainly in the Barents Sea part of the range, though it could attack the Far Eastern ringed seals too. The same is true of the killer whale (Wilke, 1954). Among the other probable enemies are the walrus; the rapacity of this animal has been reported time and again (Chapskii, 1936). There is a reference to the disappearance of the ringed seal from Rudder Bay (and from this region in general) with the arrival there of walruses (Fedoseev, 1965c). Although the walrus does attack the ringed seal here and there, it cannot be held responsible for any significant loss of seal reserves since, firstly, the walrus has survived in the USSR only in the extreme northeast and in comparatively small numbers in the Laptev Sea; in the western arctic seas, however, it is almost absent. Secondly, the ringed seal swims rather faster than the walrus and hence becomes its victim only occasionally.

From among the land vertebrates, the fox is one of the direct enemies of the ringed seal at places. Its tracks leading to the lairs of ringed seals were encountered on the coasts of Alaska (Bailey and Hendee, 1926); such instances are reported sometimes even in the Ladoga region where the ringed seal has its burrow close to the coast (S.M. Sorokin). Sometimes the wolf, too, embarks on a hunt for the pups of the Ladoga ringed seals (Andreev, 1875*; Bergman, 1956; S.M. Sorokin). In our Baltic waters large predaceous birds, especially the sea eagle, attack the young seals (Aul, Ling, and Paaver, 1957). Occasionally, ringed seals are attacked by land carnivores (at times by man too) when for some reason, although very rarely, the animals are compelled to traverse ice or snowbound land for a long time in search of open waters (see p. 246).

From among the ectoparasites of the different subspecies of the ringed seal, only one species of seal lice, *Echinophthirius horridus*, has been detected.

The helminth fauna of the ringed seal⁶⁰ inhabiting the USSR waters has been studied better than in any other zone of its range (Mozgovoi,

⁶⁰ From the same sources (see p. 208).

1953; Delyamure, 1955; A. Skryabin, 1959; Delyamure and Alekseev, 1965; Delyamure, Zavaleeva, and Fedoseev, 1965; and others).

A study of the material (Treshchev, Potelov, and Zavaleeva, 1967; Treshchev and Serdyukov, 1965; and N.V. Yurakhno) from the ringed seals of the White, Barents, Chukchi, Bering, and Okhotsk seas established 25 species and 5 larval forms of helminths in this animal. Among the trematodes, *Orthosplanchnus arcticus* infects the liver, gall bladder, and the pancreas, and is encountered more often than any other species of trematodes; the liver of one 18-year-old male from the Bering Sea revealed over a thousand specimens of this trematode (N.V. Yurakhno). *Pseudamphistomum truncatum* parasitizes the liver while *Phocitrema fusiforme* inhabits the intestine. The following cestodes were detected in the intestine: *Tetraboathrium* sp., *Anophryocephalus anophrys*, *Trigonocotyle skrjabini*, *Trigonocotyle* sp., *Diphyllbothrium lanceolatum*, *D. hians*, *D. fasciatus*, *Diphyllbothrium* sp., *Diplogonoporus tetrapterus*, and *Pyramicocephalus phocarum*. The nematodes infecting the stomach and intestine are *Contracaecum osculatum*, *Terranova decipiens*, *T. azarasi*, and *Phocascaris phocae*; *Ph. netsiki* and *Anisakidae* g. sp. infect only the intestine; *Otostrongylus circumlitus* and *Skrjabinaria spirocauda* parasitize the heart, lungs, and blood vessels while *Parafilaroides arcticus* and *P. krascheninnikovi* parasitize only the lungs; *Phocascaris phocae* infects the ringed seal more often than any other nematode. The following acanthocephalans infect the intestine: *Bolbosoma nipponicum*, *Corynosoma strumosum*, *C. semerme*, *C. validum*, *C. hadveni*, *C. ventronudum*, and *Corynosoma* sp.

A comparison of the helminth fauna of the subspecies *Ph. (h.) ochotensis* and *Ph. (h.) krascheninnikovi* established that, in addition to the common species of helminths, some are known to infect only one of the subspecies. In particular, *Phocitrema fusiforme*, *Diphyllbothrium lanceolatum*, *Anisakis* sp., *Otostrongylus circumlitus*, *Corynosoma* sp., and *Bolbosoma nipponicum* are not found in the Bering subspecies (*Ph. h. krascheninnikovi*) while, on the other hand, *Diplogonoporus tetrapterus*, *Terranova* sp., *Skrjabinaria spirocauda*, *Parafilaroides arcticus*, *P. krascheninnikovi*, *Corynosoma hadveni*, and *C. ventronudum* are not found in the Okhotsk ringed seal.

The results of a study of 220 Bering ringed seals (N.V. Yurakhno) revealed that helminths are found even among the yearlings, 90% among one- and two-year-old animals, while 100% of the animals are infected from the third year onward. Infection is particularly intense at 7 to 10 years of age. The colon (in 79.5% animals), rectum (70.4%), small intestine (68.1%), rarely the stomach (9.1%), liver (9.1%), lungs (6.8%), and heart (2.3%) are often infected.

194 The results of a study of 138 Okhotsk ringed seals (N.V. Yurakhno, V.V. Treshchev, S.L. Delyamure, A.M. Serdyukov) revealed that helminths attack animals of all ages, particularly and intensely those in the first three years of age. The body parts more often infected are the small intestine (66.6%) and colon (44.1%), and rarely the lungs (10%) and stomach (9.1%). Apart from the other pathogenic species, the nematode *S. spirocauda*, infecting the heart, blood vessels, and lungs, deserves special attention. A large number of these nematodes infect not only the adults, but also the one- and two-year-olds and cause severe emaciation in them. Heavy infection probably leads to the death of ringed seals (Delyamure, Zavaleeva, and Fedoseev, 1965).

There are undoubtedly other factors for the mortality of ringed seals: diseases (not as yet understood), adverse birth conditions, and disruptions of lactation, compression and hummocking of ice which can crush not only the pups, but also older animals, washing away of the newborns by waves or drowning of those on small ice floes in broad open water pools. The total loss, including natural mortality and commercial killing of various age groups, has been assessed only for the Okhotsk ringed seal as follows (approximate): 40% of the pups are lost in the first year (3.3% by commercial killing). In each of the subsequent 12- and 13-year-olds, about 10-13% perish, in 14- and 15-year-olds roughly 30% each, in 16- and 17-year-olds over 50% each, in 18- and 19-year-olds about 78%, in 20- to 25-year-olds over 90%, and in the older age groups wholly, i.e., 100% (Fedoseev, 1964c*, 1965f).

The ringed seal, in principle, has no serious competitors for food from among the other seals. It is quite possible that in the autumn and early winter months, the Greenland and bearded seals which thrive on polar cod compete with the ringed seal at places in the Barents and White seas. But the polar cod is so abundant that it leaves a large surplus after meeting the requirements of not only these species, but also the white whale and other animals. The common seal, i.e., the larga, can hardly be regarded as a serious competitor of the ringed seal in the Far Eastern seas since the ringed seal consumes mainly the small varieties of fish available in schools.

Population dynamics. This aspect has not been adequately studied and some comments can only be made with regard to the Okhotsk ringed seal and its intense hunting from the latter half of the 1950s and almost throughout the 1960s. From the years of the postwar restoration of hunting using ships in the Sea of Okhotsk to the early 1950s, an average of 6,000 animals per annum was taken without disturbing the delicate balance of the herd. From the mid-1950s, the position underwent a sharp change: the scales of hunting rose ten-fold to about 60,000 animals for

six years, touching a record of over 70,000 animals in 1960. This year represents the turning point and the kill began to drop thereafter. The smaller average number of animals caught per ship also served as proof of the diminishing resources. While it was 6,500 in 1957, it had dropped to 3,500 by 1963.

The unfavorable state of the population of the Okhotsk ringed seal is also witnessed by the low average age of the animals caught (6.5 years) and also the fall in the relative proportions of all generations aged 18 years or more to less than 1% (Fedoseev, 1966a). It should be remembered that the total life span of the ringed seal, judging from the Canadian populations (McLaren, 1958), exceeds 43 years. All of this viewed together points to excessive killing of these seals.

The status of the ringed seal reserves in other regions of our range suggests no such danger⁶¹ since hunting even at places where it is quite stable does not threaten the herd with degradation.

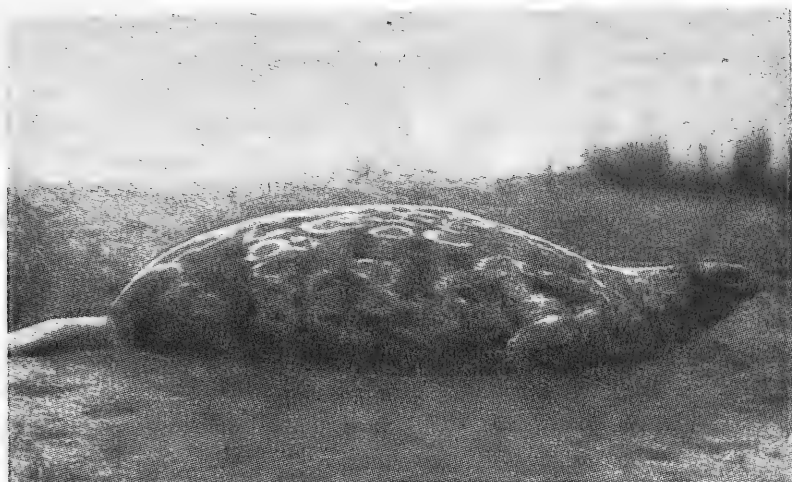
Field characteristics. These are relatively small seals, not longer than 140 cm (*Lcv*), inhabiting the arctic seas, and also Lake Ladoga. They do not form dense herds, remain on the shore ice in winter, and build snow lairs and air holes in stationary ice floes. The skin usually has a predominant pattern of fused light-colored rings with no dark-colored specks or dabs. The snout is short (Fig. 119). The claws of the fore flippers are relatively massive with a high dorsal longitudinal ridge. (K.Ch.)

Economic Importance

The economic importance of the ringed seal is quite significant and diverse. Its skin at places even now is used in the local rural economy for making nearly waterproof shoes (aviator boots, bags, slippers), mittens, caps, and jackets. In the past the skins were cut into strips to meet various needs right up to weaving them into nets. Fox hunters caught the ringed seal and even now use it as bait. It has immense importance as a source of animal food and at places even as meat for human consumption. At present, the skins are used for making superior and extremely trendy furs in the natural state for caps, dress jackets, coats, and other fur products. For this purpose animals with extremely short wool, i.e., growing or adult, are almost exclusively used.

The adverse economic implication of this seal as a consumer of commercial fish is extremely insignificant since it feeds on crustaceans and small fish which are of minor economic value (see above). Unfortunately, however, the intake of salmon by the ringed seal has been exaggerated

⁶¹ Apart from Lake Ladoga in which the population is not high.



195 Fig. 119. Large adult Ladoga ringed seal, *Phoca hispida ladogensis*, on its back (hunter's catch).

or is even altogether baseless since this seal is usually not attracted to salmon.

The main source of the ringed seal for fur and meat is the Sea of Okhotsk. Here an average of 50,000 animals were caught annually in the early 1960s (including catches by state ships and coastal collective and state game farms). Hunting by the local population on the Chukchi coasts occupied second place. From 1934 through 1940, the annual kill there ranged from 19,000 to 37,000 animals (average 25,000). In the 1940s, it varied from 14,000 to 29,000 (average 23,500), and in the 1950s, from 11,000 to 20,000 (average for the last five years of the 1950s, 15,500 per annum) (P.G. Nikulin).

196 Accurate statistics of the catch of ringed seals are not available for the White, Barents, and Kara seas. According to incomplete data, in 1933, these seas yielded a total of about 26,000 animals (nearly equal numbers from the Kara and the other two seas taken together) while in 1962, the total (partial count) kill was only 17,000 animals. In the White Sea alone, for the period 1928-1931, the incomplete figures of the kill ranged from 4,800 to 7,400 animals (Yu.I. Nazarenko). In 1960-1967, according to the approximate data based on average weight of skins with blubber, the kill in the five hunting sections of the Cheshsk-Pechora region varied from 1,800 to 9,000, an average of 5,000 ringed seals per year (A.P. Golenchenko).

In the arctic seas of Siberia, hunting is not well developed; the ringed seal is hardly caught in large numbers on the southwestern coasts of the Kara Sea in Yamal, Yenisey Bay region, and at places in the east. In the Kara Sea up to 2,000 ringed seals are caught annually to meet local requirements (V.A. Potelov).

In the Lake Ladoga region, at the beginning of this century (from 1909 through 1918), 436 to 1,278 ringed seals were caught annually. Hunting in subsequent years varied in a nearly similar range. Thus 677 animals were caught in 1928 and 1,262 in 1930 (Gottberg, 1927, 1930*; Chapskii, 1932*). From 1941 right until now, no systematic hunting has been carried out for the ringed seal. Small groups of hunters move on the ice but the kill is extremely small. Animals are trapped in large numbers in fishing nets or are caught by chance. On the whole, a few hundred ringed seals at best have been caught in recent years.

The kill of the ringed seal on the southern coasts of the Gulfs of Finland and Riga is slightly more; hunting here is undertaken by the cooperatives of collective farms.

The hunting methods are quite diverse but essentially similar to the methods used for catching other species of seals though there are some local variations.

In the Sea of Okhotsk the vast majority of the ringed seals are caught using boats dropped from hunting ships, which move among drifting ice floes, mainly in the western regions of the sea. Brigades of hunters, masked to some extent, approach the animals resting on the ice and shoot them with rifles. The coastal collective and state farmers often hunt for the ringed seal in this manner without a floating base, i.e., a hunting ship. At places, the hunters chase an animal sitting on the coast and, after a successful shot, transport it quickly to shore in a light boat.

The winter-spring hunting on shore ice (in summer at places in the arctic) is somewhat similar to the above method. The hunters go up to the edge of the hard shore ice using dog or reindeer harnesses or simply on skis, but when the shore ice is not wide enough, they reach there on foot. In order to reach a killed seal on the shore ice, a light boat or canoe is used or if the kill is close to hand, a harpoon. On the Chukchi Peninsula typical tools are used for this purpose, such as a pear-shaped stump lined peripherally with sharp hooks and tied to a branch or a frame. The hunter casts this tool at the floating body, snags it, and draws it toward himself.

In spring, when a ringed seal is resting on an ice floe near a hole, the hunter, hidden in a concealing device, crawls toward it within shooting range. He often uses various types of shields set up on a sledge or on skis.

In winter-spring, much before the ringed seal emerges onto the ice floe surface, the hunters set out with dogs in various regions, most often in the Baltics and in Lake Ladoga. The dogs help them locate the seal's air hole or lair with pups inside. Often, using the pups as bait, the hunters attempt to catch the suckling mother.

There are many methods of trapping ringed seals using nets. Special nets, with or without frames, often in the form of a sieve, are placed under the ice floe near or under an air hole or in open water pools in the shore
 197 ice. Trapping in nets (called in the western Soviet arctic "yundas" or "kryuks") is particularly widely adopted in autumn. The net, in the form of a wall, is set up at an angle to the coast and is fixed at its farther end with an additional crowd net with inward corners (or simply turned at the end toward the shore and later bent once again toward the wall). Thus a very good trap is formed; the seal encountering the net wall is snared and cannot escape. In the White and Barents seas, and at places in the Kara Sea, not only the ringed seal, but even the bearded and Greenland seals, and sometimes even white whales get trapped in such nets.

The ringed seals of the western region of the Soviet arctic are 110-130 cm long and weigh 40-65 kg. They yield 20, or almost up to 30, kg of fat with the skin. The weight of such blubber varies in different animals depending on their seasonal well-being, which is highest at the beginning to the middle of winter. In the better fed animals the blubber weighs 40 kg, more in exceptional cases. Among adults or near-adults, the average weight of the "fat in the skin" goes up to 25-27 kg: the average weight of the blubber among 130 animals caught in February was 27 kg on the Timansk coast of the Pechora Sea (Moskalenko, 1945) and 25 kg for the ringed seals of Cheshsk-Pechora region in the 1960s (A.P. Golenchenko). The blubber accounts for 50% or more of the total body weight. The skin of the ringed seal is now mainly valued as a raw material for fur. Its unprocessed weight, without the flippers, for a young animal 100-110 cm long (*Lc*) varies from 1.9 to 2.7 kg (average 2.3 kg) and in adults about 3.0 kg. The eviscerated fleshy carcass weighs 10 to 15 kg in the case of a young seal (older than a year) to about 20 kg in the case of an adult animal. The carcass without the viscera of the Pechora ringed seals caught in winter weighs around 19 kg (Moskalenko, 1945).

Seal hunting should be developed in the following main directions:

1. Rationalization of hunting the Okhotsk ringed seal to obtain the valuable fur and fat material in quantities that will not result in the decimation of the animal resources. Simultaneously, ancillary products such as the edible meat and so forth should be fully utilized (Tikhomirov, 1963).

2. Extending seal hunting into the White Sea and, in the western regions of the Soviet arctic, into the Barents and Kara seas, and also onto the Chukchi coasts and the eastern regions of the East Siberian Sea.

3. Universal standardization of hunting norms everywhere and prescribed hunting seasons (with hunting proscribed during the periods of parturition, lactation, and molting).

4. Protecting the seal reserves from unproductive losses by banning the shooting of the ringed seal in water in summer and autumn, encouraging the trapping of seals using nets, etc.

Extensive investigations on the ringed seal in all the important regions of its habitat are essential. (K.Ch.)

CASPIAN SEAL

Phoca (Pusa) caspica Gmelin, 1788

1788. *Phoca vitulina* var. *caspica*. Gmelin. Systema Naturae. Ed. XIII, 1:64. Caspian Sea.

1929. *Casiopusa behningi*. Dybowski. Bull. Intern. Acad. Polon. des Sc. Cracov, 11, No. 8-10, p. 414. Caspian Sea (nom. nud.).

1929. *Casiopusa kisielewitschi*. Dybowski. *Ibid.*, p. 414. Caspian Sea (nom. nud.).

1929. *Casiopusa dierzawini*. Dybowski. *Ibid.*, p. 414. Caspian Sea (nom. nud.). (V.H.)

Diagnosis

The body length including the tail along a straight line (*Lcv*) does not exceed 150 cm and along the dorsal side (*Lc*) up to 160 cm. The color is mottled; dark spots are interspersed on a light-colored main background, of which only narrow winding gaps remain at places (on the dorsal side). The condylobasal length of the skull is not more than 190 mm and the rostral part (from the anterior edge of the skull to the commencement of the orbits) exceeds the length of the orbits (from the anterior edge of the zygoma to the posterior wall). The tympanic bullae are small and wide-set; the gap between them is more than their length, but not more than 33 mm. The width of the bony lobe of the external auditory meatus is less than the distance from its anterior edge to the crest of the articular fossa. The anterior edge of the zygoma is usually considerably wider than the posterior one and is forked. The molars and premolars are small and set far apart; the accessory cusps on the lower jaw teeth,

commencing from the second, diverge from the main cusp. The greater and lesser tubercles on the humerus (*tuberculus majus* and *t. minus*) converge and fuse, forming a compact ring through which the tip of the biceps muscle passes. (K.Ch.)

Description

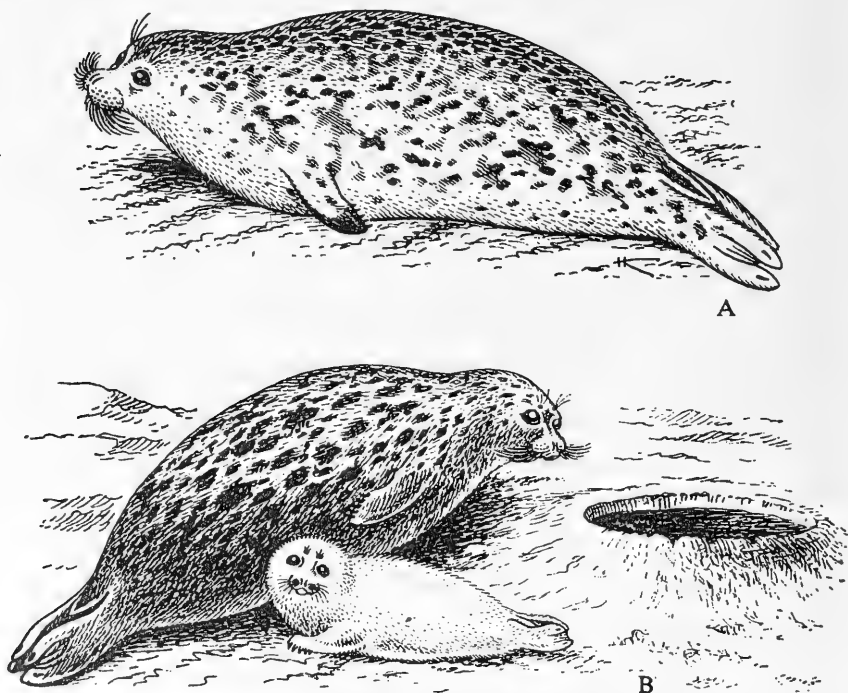
The general build and the relative dimensions of the flippers are essentially similar to the corresponding features among the closely related species, i.e., ringed and Baikal seals. The first two digits (or only the first) of the fore flipper are longer than the remaining ones and become shorter toward the fifth. The claws on them are well developed but not broad, with a rounded dorsal ridge (rib), and not greatly elevated. The neck is perceptible and does not narrow. The head is small, with a rostrum that is extended somewhat more than in the other species of the subgenus. The whiskers are flattened, with wavy edges. The labial whiskers are generally disposed in eight rows. In the first and the fifth row (counting from below), there are more often nine whiskers each; from the second to the fourth 11 to 13, and from the sixth to the eighth six (rarely seven) to 1-2. The total number frequently is 66-67 (on each side). The supraorbital whiskers number seven each and those around the nostrils one each (Yablokov and Klevezal', 1964).

The color of the hair coat varies, depending on age and sex, and also from animal to animal. Most adults are characterized by fairly intense mottling, especially on the dorsal side of the body. Because of this, the coat is considerably lighter on the belly side, more so in females. The haphazard dark gray, brown, dark blue, and often nearly black spots of various sizes and shapes, sometimes isolated and sometimes with fused edges, sometimes overlapping each other, form diverse fanciful patterns on the back of the neck, on the shoulders, and on the back. In many cases the spots are so profuse that only narrow and winding light-colored streaks remain of the main background, sometimes resembling longitudinal half-closed or closed ringlets. Spots are perceptibly rarer on the flanks (see color Plate II).

The spots on the belly are usually smaller and paler, soft brownish-gray, and their outlines less sharp and indistinct, as a result of which the underside of such animals is perceptibly lighter in color than the upper side. In most adult males, even the belly side of the body is variegated with contrasting dark brown fanciful spots. The flanks usually sport a transitory type of coloring; the dark color gradually turns lighter and descending from the back fuses with the whitish coloration of the belly running from the opposite side.

The fore flippers are sometimes more, sometimes less dark gray on the outside with minute dark gray (almost black among adult males) spots and dabs; their underside (lower side) is the color of the belly, usually without spots. The outer side of the hind flippers is steel-gray, usually the same as the back or even darker, sometimes with faint minute spots; their inner sides, turned toward each other, are light gray. The tail on the upper side is dark gray, blackish, usually with a light-colored fringe along the sides; the underside is ashy.

Although color differences between the hair coats of males and females is disturbed by individual variations, it is nevertheless quite noticeable (Figs. 120 and 121). The females have very dull tones and are similar in this respect to the immature specimens of both sexes. The dorsal side in most of the animals is a dark gray, with an olive shade, usually with an indistinct, slightly contrasting, spotted pattern, but is sometimes quite mottled. The ventral side, however, is very light-colored, grayish, with a few rather small pale brown spots or altogether without them. The spots on the fore flippers of females are either very few or absent.



199 Fig. 120. Caspian seal, *Phoca caspica*. A—adult male (with variegated colors); B—adult female (mother) with pup (figure by N.N. Kondakov).



Plate II.

Caspian seal, *Phoca (Pusa) caspica* Gm. In the foreground is an old male ("kontsy"'), behind it an adult female (mother); in the background, young animals (males and females, juveniles). Behind the female are two dark-colored juveniles; on the right is a "red-snouted" juvenile (figures by N.N. Kondakov).

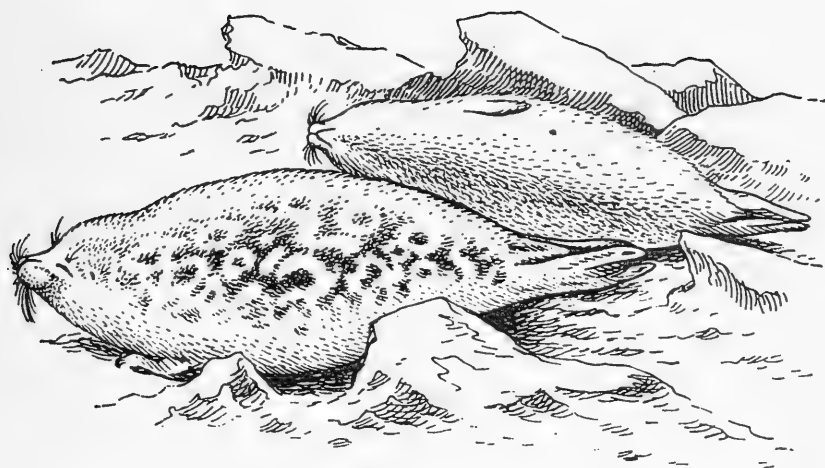
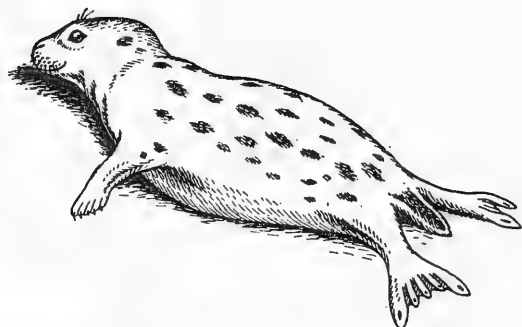


Fig. 121. Juvenile Caspian seal, *Phoca caspica* (figure by N.N. Kondakov).

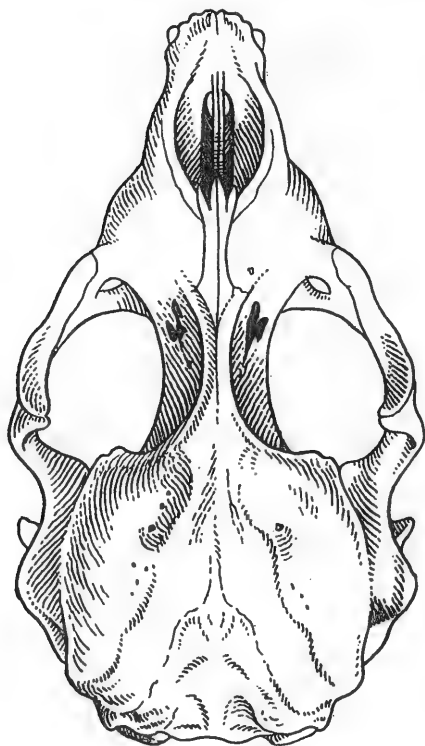
The males have a more complex and contrasting pattern on the dorsal side (which is why they are called “animals with variegated coloring”); further, the spots are more often of diverse colors, from brown to almost black. The flanks and the ventral side are also mottled with spots of various sizes; small numbers of them usually fuse together though not as densely as on the back.

The individual color variation in all age groups of both sexes is also significant. It is difficult to find two skins, especially of adult males or females, which are identical in all the design features. The form, size, number, and even the color of the spots on the ventral and dorsal sides of the body vary in the males; the color of the ventral side is particularly variable among the females. Light-colored streaks on the upper side of the body (when they are present), speckles on the flippers, and also the spotted pattern on the occiput and neck vary extremely in both sexes. Insofar as seasonal color variation is concerned, the color after molt turns brighter and is more lustrous. After summer the color becomes somewhat dull and the spots lose their sharpness.

The skull (Fig. 123) is more elongated and relatively narrower than that of the ringed seal, with a small and rather narrow cranium whose width above the mastoid processes is nearly equal to its length measured up to the orbits, but more often somewhat less. The zygomatic arches are moderately separated, hardly exceeding the width at the mastoid processes and forming not more than 110% of the latter in adults. The width of the skull at the level of the upper canines in adults is 27-29% of the



201 Fig. 122. Fetus of a Caspian seal at the end of embryonal growth (figure by N.N. Kondakov).



201 Fig. 123. Skull of Caspian seal, *Phoca caspica* (figure by N.N. Kondakov).

mastoid width; the length of the tympanic bullae is roughly 18% of the condylobasal length and varies in the range of 27-30 mm. The nasals are

long (20-25% of the condylobasal length) and narrow (width at the base of the apex 15-18% of the total length), their anterior edge terminating in three angular projections, of which the middle one is sometimes barely bifurcated and shorter than the lateral ones in most cases. They wedge into the frontal bones to one-fourth to one-third their length. The uncinat processes of the pterygoid bone are highly elongated and rather low. They terminate anteriorly with an elongated pointed projection. The posterior edge of the bony palate bears a deep arcuate notch, quite often assuming an angular form at the apex. The compact longitudinal bony septum in the choanae is faintly visible and runs posteriorly not beyond the very beginning of the palatine bones.

The upper premolars, commencing from the second, have a highly prominent main cusp and two weakly developed additional cusps; sometimes the anterior cusp is totally lacking and the posterior one better developed; one more cusp is faintly visible behind the posterior cusp. The upper molar has two cusps; it is usually separated from the fourth premolar by a prominent diastema, larger than the gap between the rest of the teeth. The corresponding lower premolars have better developed accessory cusps than in the upper teeth; one of these accessory cusps is anterior and usually two posterior. The true lower molar bears three cusps.

Sex-related differences in the skull are manifest mainly in the slightly wider rostrum in males at the level of the upper canines and in the ratios between the length and width of the tympanic bullae: in males these are slightly longer than wide (length averages 29.7 mm and width 28.8 mm) while in females these values are identical (average 28 mm) 201 (Yu.K. Timoshenko). Moreover, in males the upper maxillary bones form a more prominent bulge anterior to the orbits.

Indices of the width of the cranium and the facial length, width of the rostrum and zygoma, the first molar, uncinat processes, as also the height of the face, increase with advancing age. On the other hand, the indices of the width of the mastoid and cranium as also the height of the latter decrease (Smirnov and Chapskii, 1932).

Individual variability of the skull is fairly large both with respect to dimensions and structural features. Among these, for example, the shape of the anterior margin of the nasals is variable. Although their lateral projections are usually longer than the middle one, the latter is sometimes slightly longer than the lateral or equal to them. The form of the median process of the nasals is also variable: it is sometimes symmetrically made up of both the bones while sometimes only one bone plays a major role in its development; sometimes, it is made up wholly of one or the other bone; quite often, it is bifurcated; and in exceptional cases it may even be absent (Gadzhiev, 1957). As in many other species, the

length of the contact line of the maxillary bones with the nasal bones, the depth of wedging of the latter into the frontals, the base width of the apex and the anterior margin of the nasals, the shape and depth of the palatine notch, the length of the diastema between the fourth premolar and the first molar in the upper jaw, the number and degree of development of the accessory cusps on the crown of the premolars and molars, etc. also vary.

The body length of adults measured along the body surface from the nostrils to the tip of the tail (L_c) is generally 130-140 cm, sometimes going up to 150 cm (or even more) in the largest animals.

The body length measured in a straight line averages 10 cm less.

Sex-related differences in the body length are seen only in averages. Thus the average length (L_c) of mature (older than nine years) males is 134.2 ± 0.77 cm and of females 131.7 ± 0.47 cm (Yu.K. Timoshenko).

The total weight of the adults in the period of their utmost well-being varies from 50 to 85 kg (average 70 kg), the subcutaneous fat with the skin accounting for up to 40-50 kg. The animals attain maximum weight late in autumn and early in winter. They are impoverished by spring and their weight falls, on average, to 40-45 kg (their maximum weight at this time does not exceed 65 kg); the weight of the blubber (with the skin) 202 decreases, on average, up to 20-25 kg (more than 30-32 kg of fat in the skin is unusual in this season).

The condylobasal length of adults aged 10 or more years is 170-190 mm, the width of the cranium at the mammiform (mastoid) processes 85-100 mm, and the width at the zygoma 89-150 mm.

The size difference of the skull between males and females is not much. Among males, the condylobasal length varies from 171.6-190.3 mm ($\bar{x} = 182.1$), width at the mastoid 88.2-97.8 mm ($\bar{x} = 93.4$), width at the zygoma 91.6-104.6 mm ($\bar{x} = 98.7$), width above the canines 24.1-29.2 mm ($\bar{x} = 26.4$), and interorbital width 4.5-7.7 mm ($\bar{x} = 5.9$).

The condylobasal length among the females varies from 171.8-182.0 mm ($\bar{x} = 175.1$), width at the mastoid 85.0-95.5 mm ($\bar{x} = 89.6$), width at the zygoma 89.3-98.7 mm ($\bar{x} = 93.6$), width above the canines 23.2-27.0 mm ($\bar{x} = 24.8$), and interorbital width 4.0-6.7 mm (M 5.6) (Yu.K. Timoshenko). (K.Ch.)

Taxonomy

Genetic relations with the closely related species are defined by grouping this species in the same subgenus (or genus) with the ringed seal (*Ph. hispida*) and Baikal seal (*Ph. sibirica*). These are no doubt extremely close but the interpretation of the Caspian seal (like the Baikal) as a subspecies

of the ringed seal (*Phoca hispida* Schreb.) has not been supported by contemporary scientists.

The direct evolution of the Caspian seal has not yet been conclusively established. In fact, recent descriptions of some paleontological finds, a review of former finds, and also an analysis of the morphological features have brought this problem closer to a solution. Nevertheless, there are two main hypotheses explaining the evolution of this species. According to one, the seals colonized the Caspian Sea in the Quaternary period having somehow entered there from the north under the influence of the glaciers which displaced some part of the population of the ancestors of the ringed seal to the south. Having entered a new water body, they were ultimately transformed into the present-day Caspian seal.

With regard to the Caspian seal's entry into the Caspian Sea, some researchers assign a decisive role to the extensive freshwater body formed as a result of the significant head of river waters over the vast expanse of northwestern Siberia (Pirozhnikov, 1937; Davies, 1958). This water body, extending up to present-day northeastern Kazakhstan, encompassed the present-day Aral Sea and came close to the Caspian, with which it could have come into contact through the river streams, and came close even to Lake Baikal.

According to the second hypothesis, based on paleontological data for the Pliocene and the Miocene, the Caspian seal is regarded as a descendant of the seals of the subgenus *Pusa* inhabiting the successively superseded Sarmatsk, Meotichesk, Pontichesk, and other basins, leading ultimately to the formation of the present-day Caspian Sea. Several fossil finds of Upper Tertiary and Early Quaternary seals from along the periphery of the Caspian and in other southern regions reveal features of close genetic affinity with the present-day Caspian seal. The second point of view received fresh substantiation in the last decades (Chapskii, 1948, 1955; Gadzhiev, 1959; Kirpichnikov, 1964). Evidently there is greater justification for the hypothesis of the autochthonous evolution of the Caspian seal than for considering it as having arrived from the north.

All the three branches of seals of the subgenus *Pusa*, i.e., the Caspian, Baikal, and ringed seals, became isolated presumably at the end of the Tertiary and embarked on a long course of independent development. (K.Ch.)

Geographic Distribution

The geographic distribution is limited exclusively to the Caspian Sea, from which some rare strays into the Volga and Ural have been recorded.

A good number of seals are encountered in some seasons throughout the sea, from the coastal regions of the northern Caspian to the Iranian coasts. They are widely distributed throughout the sea in summer, at the end of the breeding and molting periods. Then they are found simultaneously in various regions of the northern shallow waters, right up to the northeastern extremity of the sea, in the region of Tyulen' archipelago (Kulaly, Morsk, Rybachii, Podgornyi, Novye, etc. islands north of Mangyshlak Peninsula), on the western side of the sea (commencing from the prodelta of the Volga to Lenkoran and farther south), and along the eastern edge of the sea from Mangyshlak to Atrek and more southward (except in Karabogazgol), and also in its central parts.

The nature of the summer-autumn distribution of the seals is dependent on food conditions. Concentrations of schools of fish and other edible items can bring about fairly intense concentrations of seals at times, although they are thinly dispersed in the summer season. In the northern part of the sea, sporadic concentrations are seen on Zhemchuzhnykh, Rakushechnaya, and Kulalinsk banks and additionally between Cape Urdyuk and Kendirli Bay during massive concentrations of sprat there (Badamshin, 1948). By autumn, they are confined preferentially to the northern Caspian at places of feeding as well as in regions of island rookeries. Autumn concentrations are particularly regularly seen on small dry islands with shell and sandy shores (shalyg and "pleshina") in the northeastern corner of the sea at Karatonsk, Suendykovsk, Balashovsk, Kolkhozhnye, and Borozdinsk, and also on the Zyuidvestov Islands in the fore-estuary of the Ural, Utaespinsk, and Kulalinsk Rivers, and on Malyi Zhemchuzhnyi Island (B.I. Badamshin). The seals gather in the southern Caspian on the islands of the Apsheron archipelago and on Ogurchinsk. They live in relatively small numbers on all the above islands in summer also.

The period of autumn concentrations of seals in the region of bald patches extends usually from September to the time of complete freezing. In winter most of the population is concentrated in the icebound northern part of the sea but occasionally stray animals and small groups are encountered at this time even in the more southern regions of the sea. From spring, on the contrary, most of the population migrates southward and is dispersed over wide expanses in the central and southern Caspian (see p. 270).

Geographic Range outside the USSR

Covers only a narrow strip of the southern Caspian in the territorial waters of Iran. (K.Ch.)

Geographic Variation

Not reported.

Biology

Population. It was impossible to make a direct count of the population of the Caspian seal until the early 1970s and only indirect indices were used for estimations. These indices are the stability or dynamics of the annual catch, areas of the nurseries, counting from ships the number of animals sighted in the water, etc.

204 In the past, when hunting exceeded an average of 100,000 animals per annum for 90 years (1824 through 1915), the population of this seal was large and evidently exceeded a million.

It has not yet become possible to count the present-day population. A maximum of 750,000 animals was cited for the end of the 1950s and 470,000 for the mid-1960s (Badamshin, 1960, 1966). Even a figure of 600,000 was advanced for this period (Chapskii, 1966).⁶² The latter two figures represent the main reserve, i.e., the population before breeding (without pups of the current year). One of the fairly reliable bases for these calculations was the position prevailing in the hunting season at the beginning of 1966 when, supposedly, 88,500 pups were killed. But even then, the population was calculated largely on arbitrary assumptions of the percentages of the rest of the herd constituents: quantitative proportion of immature animals of both sexes and productive animals. The figure of 500,000-600,000 is perhaps quite close to the present-day size of the herd.

Habitat. The Caspian seal is not very particular about its habitat conditions (aquatic). It is found in very shallow water regions and in the zone of extremely large depths along the coasts as well as in the pelagic sections of the sea. It is biologically associated with ice floes on which it breeds and suckles the pups and also spends much of the molting period. It has no special requirements for the ice floes except that they be quite stable. Land is also used for setting up rookeries: bald patches as well as sandy-pebbly and rocky coasts of islands. These seals avoid coasts overgrown with reeds and other vegetation. They are not very fond of the rivers though they ascend the Volga in rare cases up to Astrakhan and even up to Volgograd (Badamshin, 1966). They are obviously not very timid and do not avoid waters with fairly active shipping; for example,

⁶² Some foreign publications (Scheffer, 1958; King, 1964) put the Caspian seal population at 1.5 million, a figure communicated at one time by these authors to S.V. Dorofeev.

they enter Tyub-Karagansk Bay (in Port Bautino). They, however, select deserted, isolated, and uninhabited islands, and bald patches for forming coastal rookeries.

Food. These seals feed throughout the year evidently without prolonged or total interruptions but with varying intensity in different seasons. Feeding is not very intensive in late autumn, winter, or early spring nor in summer although this phenomenon is manifest to different degrees in different groups. Animals undergoing parturition and suckling mothers feed less regularly and sometimes probably remain half-starved. On large-scale autopsy of adult seals caught in the nurseries in February, food was found in nearly all the stomachs (Dorofeev and Freiman, 1928) and only a few (Roganov, 1931) contained a small amount (five of 30 animals autopsied). Similar observations were reported even later (Badamshin, 1948; Kurochkin, 1958) and hence it is hardly an exaggeration that, after winter, the half-starved seals "starved in the winter, rush to feed" in the spring (Kurochkin, 1958). However, in early spring, during the molting period, feeding is even further weakened due to prolonged resting of the animals on floating ice floes, ice mounds, and later even on bald patches. At this time, food remnants were detected in 8 to 16% (Badamshin, 1948) and sometimes in 30% (Roganov, 1930) of the seals caught. From mid-April, the seals abandon the ice floes and bald patches in the northern part of the sea and take to even more intensive feeding, especially along the coasts of southern Dagestan in the second half of April and in early May.

In the autumn-winter period, in Mangyshlak region, even in years of
 205 fish abundance, the seals fed almost exclusively on trash fish or fish of low commercial value, and also on crustaceans and some other invertebrates. Of the 150 seals with food in the stomach, the majority were found to have fed on goby followed by sprat and sand smelt, and only 2% contained the remnants of pike-perch (Samofalov, 1931*). In the stomach of nearly 400 seals caught in nets in the same region and in the same months but in much later years (1939 through 1946), goby occupied first place (in 29 to 43% of the animals), sprat accounted for 3 to 30% in different years, while shrimps of different types played a major role (18 to 33%); further, 11 to 15% of the animals contained mollusks; sand smelt was found in two seasons in 1.5 to 11.0% of the animals; and herring was found in only two seals (Badamshin, 1948).

In winter, in the northern part of the sea covered by ice floes, the seals subsist exclusively on fish of no commercial value, mainly goby and various invertebrates. At the end of the 1920s, goby and amphipods predominated in the food of seals in this season; crustaceans and mollusks were consumed very rarely while commercial fishes held no attraction

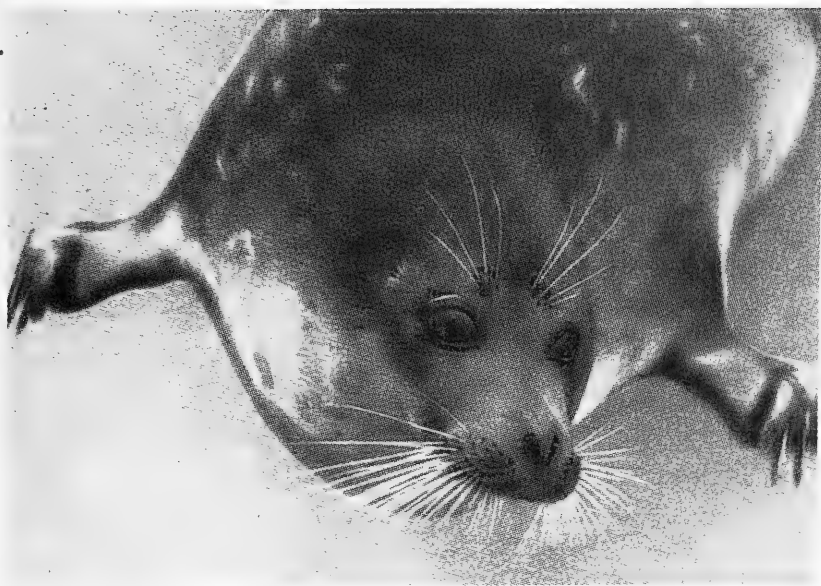


Fig. 124. Adult female Caspian seal, February, 1953 (photograph by Yu.V. Kurochkin).

at all (Dorofeev and Freiman, 1928; Terebenin, 1930; Roganov, 1931; Samofalov, 1931*; Kurochkin, 1958).

The food of these seals in spring has not been adequately studied. In earlier years the food in April consisted mainly of sprat, some sand smelt, and herring to an even lesser extent. The latter was detected in only 14% of the seals whose stomach contained food. The remaining items (small Caspian roach, sabrefish, and amphipods) formed 2% (Roganov, 1930). In the more southern regions in spring the nutritive value of commercial fishes rose somewhat, especially when their arrivals coincided with the residence of the seals. In the past this was promoted to some extent by the use of sweep nets to catch herring. In early May, 1929, on the coasts of southern Dagestan, the seals rushed to the nets, jumped into them, and quite often were trapped inside them along with the fishes (Chapskii, 1930).

206 The summer food of these seals has been studied even less. However, it is known that in summer as well as in early autumn, they are regularly seen in the regions of sprat concentrations (Badamshin, 1966).

Experiments on the prolonged rearing of seals were carried out in the basins of a fishing station in Bautino village and on Kulaly Island. The seals there had a choice from diverse fishes; goby, sprat, herring, pike-perch, Caspian roach, sand smelt, as also crustaceans—shrimps and

crayfishes. The first preference of the seals was goby and sprat and, when these were abundantly available, the animals did not turn to other fishes or crustaceans. When the goby and sprat were inadequate, the seals additionally took to herring and Caspian roach; the last preferences were sand smelt, shrimp, and crayfish (Badamshin, 1948, 1960). Evidently goby and sprat could be regarded as the predominant food of the Caspian seal. The animals initially consumed live fish exclusively but later became accustomed to dead fish and in time could be hand-fed. A young seal 105 cm long consumed in one sitting up to 100-120 sprat, i.e., 250-280 g; an hour later, it consumed an additional helping of 30-40 more. The daily ration of the seals of different ages held in the basin varied from 1.2 to 1.8 kg ($\bar{x} = 1.4$) in the case of yearlings and 3.2 kg (up to 1.2 kg in one helping) in older juveniles; an adult male consumed up to 1.7 kg in one sitting and up to 4.5 kg in one day (see p. 276).

Home range. In the conventional sense of the term, a home range is not characteristic of either single or groups of these seals. In different seasons of the year, under different environmental conditions, and to some extent also depending on the region, the extent of seal concentration is extremely variable; on a solid substratum—land or ice—it is usually far greater than in water. The spring and autumn haunts are most concentrated on bald patches, especially when a section of such projecting from the water is small. Then the animals are often packed densely. On the more extensive bald patches, 100 or more seals can be found in an area of 100 m². Somewhat more rarely than in the autumn rookeries, but no less densely, the seals are disposed even in spring at the time of molt on icy hummocks and drifting ice floes. On the latter the animals rest only on the extreme edge, usually in single file, head facing the water, in the form of a typical border extending for tens and sometimes hundreds of meters.

The lactating females (mothers with pups, Fig 125) on the ice floes of the northern Caspian are usually much less compact. Pairs disposed at intervals of 5-6 to a few tens of meters and sometimes even farther apart on the wide expanse of the ice floes, create the impression of a typically large, highly scattered, herd. But the herd is nowhere united; the animals are not concentrated in any definite section of the ice floes; on the contrary, they are divided into sections on the wide expanse at fairly large intervals (see p. 280). It is this feature that renders the application of aerial photography for a quantitative estimation of the mothers or pups extremely difficult.

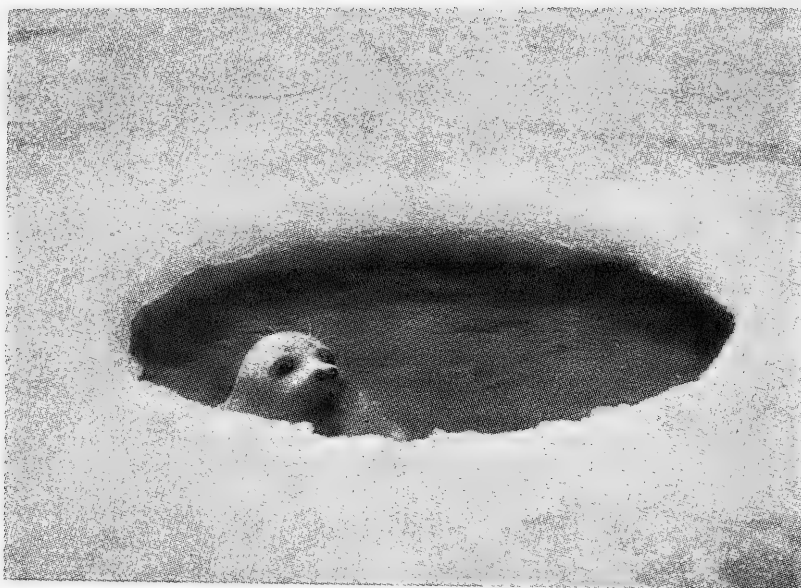
The densest concentrations of seals are seen in the water firstly in the period immediately preceding whelping, when the females ready to birth are concentrated on the more suitable ice floes; secondly, when the



207 Fig. 125. Female (mother) Caspian seal with white pup. Caspian Sea, February, 1958 (photograph by Yu.V. Kurochkin).

molting rookeries are disbanded; and thirdly in the autumn, in anticipation of the drying up of the bald patches on which the animals can gather. In all other cases the seals are distributed sparsely, mainly singly or in small groups in which one animal is separated from another by tens or even hundreds of meters.

Hideouts and shelters. Like some other seals with a biological affinity for ice floes, the Caspian seal living in water among ice floes is compelled to ensure for itself access to air for respiration and also some means for crawling onto the ice and re-entering the water. Air holes, open water pools, and cracks in the ice floes are inadequate for this purpose and the animal is thus compelled to make openings in the ice and to maintain them. They resort to such, however, only when the sections of open water surface among the ice floes is covered by a continuous crust of recently formed thin ice. When its thickness is 1-2 cm, the seals can easily pierce it from below with their head but do not necessarily use such holes (Fig. 126). If, however, the ice thickens rapidly, they use the holes made earlier. With time, depending on the thickness of the ice, these openings (air holes), like those made by the ringed and harp seals, acquire the form of a truncated cone due to constant use, narrowing toward the top and opening on the surface of the ice floe or covered by



209 Fig. 126. Caspian seal in a wide hole. February, 1958 (photograph by Yu.V. Kurochkin).

a thin icy arch. This arch is formed gradually, partly due to the freezing of the water splashed during diving, and partly by the snowdrifts thawing inside under the influence of the warm exhaled air. At the center or side of this arch is a narrow throughway 5-10 cm in diameter (Badamshin, 1948). If or when the ice cover is broken and open water pools form in the vicinity, the seals abandon their former air holes and use the open water for respiration until it is covered by an ice crust, compelling a new air hole to be made.

Later, as the whelping period approaches, gestating females scrape the air holes with their claws, widening the upper part of the cone in the same manner, and transform the initial air hole into a lair which is used later for crawling onto the ice and re-entering the water throughout the lactation period. The same lair is often used by several animals. The Caspian seal makes no other hole or lair in the snow or in the icy hummocks for the pup, preferring to undergo parturition directly on thick stable ice floes with hummocks that can protect the newborn from the winds.

208 *Daily activity and behavior.* These aspects are even less studied. The daily activity and behavior are closely dependent on the seasonal periodic phenomena which, in the life of the Caspian seal, proceed in the

same sequence as in the case of other species. The commencement of the calendar year marks the period of high activity. The seals have to acclimatize to the formation of ice floes; the adult animals are concentrated in the breeding zone and the females on the eve of whelping look out for appropriate sites. The "nursing" period involves the care and suckling of the pup, which conforms to no daily rhythm of activity as at other times. The mating period follows thereafter.

With the conclusion of these stages of the annual cycle, a relatively more quiet molting period sets in. The animals rest on the ice floes for long periods and later on the bald patches in the same region, lost in sleep and drowsiness that is interrupted rather rarely and at irregular intervals for food intake.

The origin of early rookeries on the northern bald patches is evidently related to weather conditions. They are formed by the same groups of seals which have not been able to complete molt by the time the ice floes have thawed (see p. 282). After severe and prolonged winters, these rookeries are formed only in May while, after normal or mild winters and in early spring, they are formed even by April. The spring rookeries are usually active for not more than a month and comprise three-fourths juveniles of both sexes and one-fourth adult females; the adult males in them do not exceed 0.5%. The animals are found on bald patches even in summer but their concentrations at that time are unstable and less numerous and consist predominantly of juveniles; they gather at night and usually go into the water in the morning (Badamshin, 1948a, 1950).

Thus these contingents, like the other seals which have completed molt early, again enter a period of high activity in the second half of spring. Throughout the rest of summer, up to mid-September, they are seen in the water scattered singly or in small but sparse groups. They can sleep in water as well as on land. Their activity at this time depends mainly on their appetite, which continues to be voracious until they are fully satiated. Summer and part of autumn represent the most important period of feeding, when the animals not only recoup their fat reserves, but also accumulate them to face the oncoming winter.

In the basin satiated animals sleep for hours quietly, only sometimes turning from one side to the other or from the back onto the belly. Hungry animals, however, are restless and very active (Badamshin, 1948b*, 1960).

In autumn, having fed themselves fully, the seals once again turn to land, particularly to bald patches in the northeastern part of the sea, but their activity has sharply decreased by this time. As long as the bald patches are covered by high water, the seals swim leisurely in their proximity or lie immobile on the surface in anticipation of their exposure by

a surging wind. As soon as such conditions set in, the animals crawl onto the shoals, which are quite often covered completely with their bodies. On quiet nights, discordant sounds can be heard occasionally from this crowd and various minor skirmishes occur here and there (inevitable in close living quarters). The seals sleep most often on the side, but quite often on the back or belly. The neck is foreshortened, the hind flippers extended, and the fore flippers pressed close to the body. One of the hind flippers often forms a fist and is concealed by the other. From time to time, for short intervals, the hind flippers are opened out fanlike, then dropped limply but extended to the ground. Then the seal raises its head and hind flippers high, as though stretching, bowing its body, then once again resumes its original posture. On clear, sunny days the seals rest a long time on the bald patches; in cloudy weather, especially in
 209 rainy weather, they become restless or leave the bald patches altogether; a thunderstorm drives them into the water (Badamshin, 1948).

The autumn rookeries on the northeastern bald patches comprise males and females of different age groups but productive males and immature animals of both sexes predominate in them. Mature females are relatively few.

Like the autumn rookeries, the spring-summer island rookeries formed in the 1930s in the south, especially in the region of the Apsheron archipelago, also consisted almost exclusively of adult males with a negligible admixture of juveniles of different age groups. Adult females appeared only as solitary individuals (Kleinenberg, 1939).

The seals are naturally afraid of man, especially in the rookeries on bald patches. However, by assuming the posture of a lying animal and moving quietly, one can crawl close to them. The self-preservation reflexes are poorly developed among the young compared to the adult. Instances of the inexplicable gullibility of the animals have been recorded. Thus in the autumn of 1959, one yearling that had evidently strayed from the herd onto a bald patch, repeatedly attempted to get onto a drifting ship, apparently because of its overpowering need to find land.

Seasonal migrations and transgressions. The Caspian seal undertakes extensive migrations annually and with high regularity. In spring, with the thawing of drifting ice floes in the northern Caspian, the bulk of the seals concentrated there even from the end of autumn to early winter, constituting barely 0.9% of the total population, begin to move gradually southward. The first to leave are the females that have undergone parturition, followed by their suckled and molted pups. Later, having completed molt, the adult males too move in the same direction; the last to abandon the northern waters are immature animals of both sexes.

This process is protracted since the movement southward coincides
210 with intensive feeding. By the end of spring to the commencement of
summer, much of the population has moved into the central and southern
Caspian Sea, where the animals, wandering from place to place, remain
until the end of summer before moving northward subsequently.

These seals migrate mostly in very sparse, small groups, forming no
close-knit herds. They do not usually move continuously in the same
direction, especially during their southward migration, but nonetheless
reach the south although the migrations appear disoriented at first
glance. There are presumably no strictly fixed routes for journeying south
and returning north. While feeding on the way, the animals move in a
broad front, some closer to the western coasts of the sea, others strictly
along the eastern rim, and some others quite far away from the coasts.
Nevertheless, the seals visit the same regions en route year after year.

The intense summer warming of the water, which evidently the seals
cannot withstand, is usually regarded as the most important factor caus-
ing their southward migration in spring from the shallow northern parts
of the sea. In the central and southern parts of the sea, because of the
greater depths and constant mixing of the water body, there is no warm-
ing up of the surface waters and hence more favorable temperature con-
ditions are created for the seals. Without doubt, the food factor also
plays an important role.

In the summer months most of the seals are confined to water, usu-
ally sparsely, and it is difficult to say where they are more numerous
at that time. According to recent observations (B.I. Badamshin), much
of the population is distributed in summer throughout the expanse of
the central and southern Caspian. Evidently the seals do not require a
solid substratum in summer. Therefore, as in the past, now too seals
are encountered in summer irregularly and, too, in tens or rarely in
hundreds in the rookeries surviving in the southern Caspian: on sev-
eral islets (oil stones) along the Apsheron Peninsula, nameless islets at
the inlet of Krasnovodsk Bay, Ogurchinsk Island, and others. With the
onset of autumn, much larger rookeries are formed at these places but
they nowhere are equal in size to those characteristic of the northern
Caspian.

With the approach of autumn, almost all the seals that have fed or
are continuing to feed begin to gradually migrate northward again. The
seals moving in this direction are abundant in the Mangyshlak region,
Tyulen' archipelago, and the extreme northeastern, highly shallow part
of the sea. Much of the population is concentrated in the northern and
northeastern Caspian even before the formation of ice floes. It is in such
places on the northeastern bald patches that the largest prewinter seal

rookeries are formed regularly at present. With the approach of winter and the first appearance of ice floes, the rookeries on the bald patches break up and the whole seal population approaching the north moves slightly southwest and is later confined mainly to the edges of the ice floes that have formed over a large area.

Concurrent with these local movements of the animals that have already arrived in the north, animals continue to arrive from the south, from the regions of the central Caspian. Judging from seals caught in nets, formerly practiced at Mangyshlak, even mothers and productive males continue to migrate northward in December and January (Samofalov, 1930).

Some seals, contrarily, join no group traveling north in autumn but remain in the south for winter. These are mainly immature animals and an insignificant number of adult males. The latter have lost the urge to migrate for some reason (probably diminution of the reproductive function) and their herd instinct (or other ecological factors caused by subordinate relations) holds them to their young.

With the approaching whelping period, gestating females enter deep into the icy environment by any possible means, search out the most
 211 stable large ice floes and, when the time for parturition approaches, crawl onto the ice. Since they migrate in herds and the season of births is not very prolonged, a large number of animals are seen on the ice almost simultaneously and quite close to each other. The first rookeries on ice floes thus initially consist almost exclusively of gestating females, with pups appearing later. The adult males remain until this time with the immature animals of both sexes near the edge; they begin to crawl on the ice slightly later and form individual, very dense, compact rookeries.

Reproduction. Like other species of the subfamily, the Caspian seal too does not form pairs for long. Because pairs are short-lived, encounters between competitors are not very serious. The natural population ratio of adult males to females is close to one but due to unilateral hunting in recent years (see p. 289), there is evidently some surplus of productive males even now (Badamshin, 1966a). However, it would be more appropriate to view the situation as a shortage of productive females.

Among females that have attained maturity but have not yet undergone parturition, though ovulating (corpus luteum present in one ovary in autumn), the uterus varies from 25 to 50 g in weight and the ovaries from 2.0-3.5 cm in length and 1.0-3.8 g in weight.

The testes of mature males are 7.5-8.0 cm in length and 20-35 g in weight (with the appendage).

The mating season commences roughly mid-February, i.e., even before lactation ceases, and ends in the last few days of the same month or in the first few days of March (Dorofeev and Freiman, 1928; Yu.V. Kurochkin and B.I. Badamshin) or even extends up to March 20 (Smirnov, 1930*). The total duration of gestation has been roughly determined as 11 months. However, the duration of active embryogeny (after implantation of the blastocyst) and that of the latent stage have yet to be fully established. Evidently they do not differ significantly from the corresponding values for other closely related species.

The whelping of most of the females occurs in a short time span of 10 days, from the end of January to about February 5. In very rare exceptions, the pups are born slightly earlier, or more often, later. In any case, the total period of whelping, with occasional exceptions, extends to no more than 20 to 25 days and ceases by February 10. Much later solitary cases of births have been reported: on February 27 (Samofalov, 1930) and even in the first few days of March (Roganov, 1931). Even greater but extremely rare deviations have likewise been reported (Badamshin, 1948). One gestating female was found on May 10, 1942, on Suendikov bald patch. The embryo was 53 cm long and, theoretically, this female should have undergone parturition roughly 1.5-2 months later, i.e., at the end of June or in the first half of July. A pup 79 cm long was caught with its mother on July 28, 1941, on Balashov bald patch. Judging from its state of intense molting, the pup was no more than 2-2.5 weeks old.

The litter of the Caspian seal, like that of the other species of Pinnipedia, consists of a single pup, two being extremely rare. At birth, the body length of the pup varies roughly from 70 to 75 cm (*Lc*) while the weight varies around 3-4 kg. The newborn is almost devoid of subcutaneous fat layer. The hair coat is usually of the embryonal type: dense, long, silky, almost pure white (with a creamy-pistachio tinge in the first few days), often with a smoky-gray bloom on the dorsal side.

The period of lactation extends evidently for about four weeks. In the first few days after birth, the mother almost does not lose sight of her pup, suckling it repeatedly at different times round the clock. Later, she leaves the pup for a long duration, thus suspending suckling for
 212 prolonged periods. The pup spends much of the time sleeping on the ice floe, and waking up, begins to look for its mother. Often, not finding her, it crawls to an air hole and peers into the water as though expecting its mother to emerge. When the wait is long, it calls in a voice resembling the wail of a child (Badamshin, 1949). To suckle the pup, the mother lies on her side or almost on her back, exposing the teats.

Until recently, there were no rational data on the age at which maturity sets in among these seals. It was assumed (N.A. Smirnov, 1931) that

the female attains maturity at two years of age and the male a year later. Similar views were expressed even more categorically (Roganov, 1931). Later, based on raising seals in an artificial basin on Kulaly Island, the view was expressed that they attain maturity at five years of age (Badamshin, 1960). Finally, by studying the reproductive organs in relation to different age-related criteria, it was demonstrated that the females commence undergoing parturition mainly in the sixth year of age (Chapskii, 1965a*).

Not all the females that have attained maturity reproduce every year but there are as yet no reliable data on the extent of barrenness. Presumably, it covers 15 to 30% of the eligible females (Badamshin, 1950, 1960).

The seals gather for breeding on ice floes in the northern part of the sea mainly in the Gur'evsk Channel region and west and southwest of it (relatively close to the edge on a strip extending roughly from the meridian of Kulaly Island to Rakushechnaya and Zhemchuzhnaya banks). Depending on weather conditions, the maximum concentration of mothers with pups is seen on all sides. Further, when the winter is mild and late and hence the expanse bound by ice floes is relatively small, the seals reproduce far away in the northeast. Because the area of ice cover is small, the region inhabited by the seals is greatly reduced and their concentration perceptibly increases. A reverse picture is observed in abnormally severe winters. The area of ice cover then becomes markedly enlarged, the rim of the ice floes extends far southwest and the bulk of the animals move in the same direction as the ice floes.

For whelping, the most stable ice floes with fairly level sections interspersed with hummocks are chosen. The females prefer the rims of such ice floes but, in their absence, are compelled to give birth even on very smooth young ice that is strong enough not only to sustain the weight of the gestating mother, but also to withstand some thrust of the ice floes in a fresh wind.

The herd instinct, characteristic of the Caspian seal, combined with the need to select the most appropriate ice floes for whelping, results in a fairly high concentration of reproducing females. Their disposition with pups on an ice floe largely resembles the nurseries of the harp seal but of smaller size and density. The animals lie widely scattered with highly dispersed groups (so-called "spots") varying in size and concentration alternating with floes uninhabited by animals.

Some spots consist of several tens to hundreds and even a thousand animals. In the gaps between the spots, often running into several kilometers, there are no animals at all or they are encountered very rarely. Sometimes, however, the spots are quite close to each other.

Growth, development, and molt. The young pup grows and develops as rapidly as any other earless seal. After a brief lactation period, the pup grows roughly 20% longer (compared to its original length) to 214 85-90 cm (L_c) while the original weight increases more than four times. It accumulates up to 8-12 kg or more of subcutaneous fat.

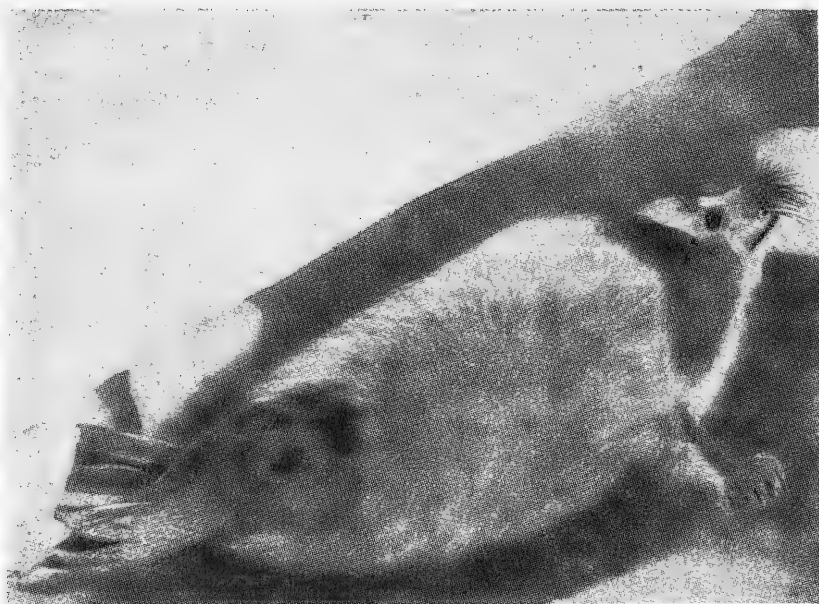
The following data describe the growth tempo of the young female: body length (L_c) at about nine months varies from 86 to 104 cm, average 94.5 cm; in autumn of the second year, the average is 107 cm; in the third autumn 114 to 119 cm (average 117 cm); and by the fourth autumn the average is 124.5 cm. Further growth is highly retarded (Chapskii, 1965a*).

In the normal course of lactation, 15-20 days after birth the belek [= white pup] begins to molt. Initially molting is barely perceptible but with each successive day, its furry white hair is increasingly shed. The coat becomes less even and shaggy and is interspersed with dark-colored bald patches and covered with the new short and bristly hairs typical of seals. In this phase of intense molting, extending roughly for two weeks, the pup is called a "tulupka" [highly molting pup] (Figs. 127, 128). En masse molting of pups usually occurs around the 10th of February and is completed in the majority of them by the end of February or the first few days of March. The pup that has completely shed its juvenile hair coat is called a "sivar". Lactation quite often ceases in the last stages of molt but often the mother suckles even the "sivar".

The upper side of the hair coat of a "sivar" is almost monochromatic dark gray; spots, even when visible, are not always very distinct. The underside is light-colored, whitish, and without spots in most animals. From year to year, with every successive molt, the spotted pattern becomes increasingly evident on the back. Spottiness is seen more sharply in males and less so in females. The color on the ventral side is also as variable: in males, with time, the number and brightness of spots increase ever more but in females the increased spottiness is usually faint, dull, and even altogether absent in very rare cases.

Molt is protracted in the first year and subsequently in all animals commencing from yearlings. In some animals it apparently continues for a little longer than a month. The total duration of molt, however, has been put variously at 1.5 months (Dorofeev and Freiman, 1928) to 2 months (N. Smirnov, 1931) and even up to 3-4.5 months (Badamshin, 1948, 1965*). Molting commences first in the females that have given birth (in many cases even during lactation); it commences somewhat later among adult males and then among immature animals of both sexes (in the so-called "zheltyaks").

Not all the seals succeed in molting on drifting ice floes; many of them are forced to continue it on icy hummocks and when these also

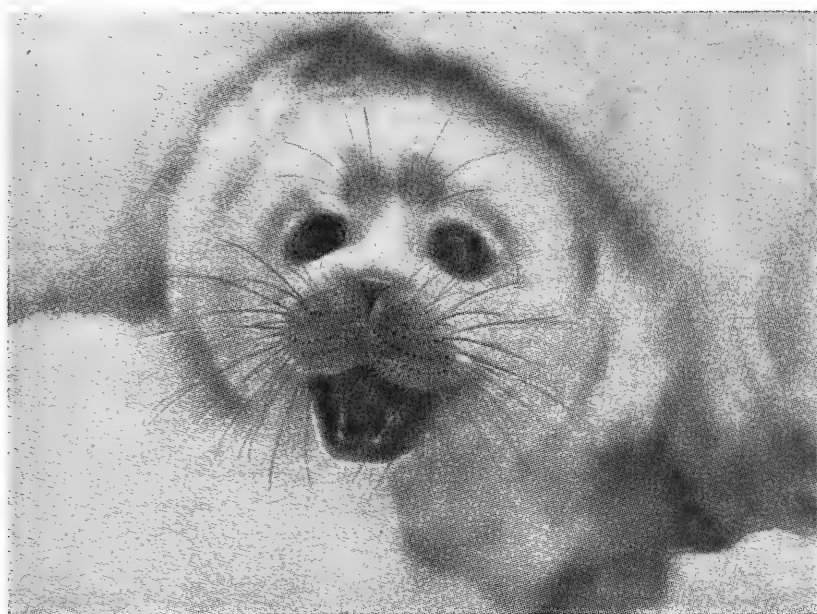


213 Fig. 127. Intensely molting young Caspian seal ("tulupka"). February, 1958 (photograph by Yu.V. Kurochkin).

break up, molting continues on bald patches and islands. Immature animals, together with a fairly good admixture of adult males, form late molting colonies. Adult females however complete molting on the drifting ice and only small numbers of them are encountered on bald patches in spring. Weather conditions play no mean role in the disposition of molting animals. When the ice floes hold for long in the northern part of the sea (which happens in very severe winters in which, evidently, the ice floes break up slowly), the seals molt on them; otherwise, when the winter is mild and the floes thaw rapidly, many animals are compelled to complete molting on land (on the northern and southern Caspian islands).

Enemies, diseases, mortality, and competitors. The factors and magnitude of natural mortality of the Caspian seal are not yet fully understood. There are no natural enemies of the seal in water, with the exception, perhaps, of large white whales which may catch very young seals from time to time.

The main enemies from among the land vertebrates are the long-tailed [pallas'] sea eagle (*Haliaeetus leucoryphus*), white-tailed [gray] eagle (*H. albicilla*), and partly the golden eagle (*Aquila chrysaetus*), but



213 Fig. 128. Young Caspian seal ("tulupka"). End of February, 1958 (photograph
215 by Yu.V. Kurochkin).

their role as enemies of the newborn is hardly significant. Foxes and
215 wolves rarely pursue the seals on ice and the damage caused by these
predators is perhaps extremely small, though it has been mentioned in
the literature (Khastatov, 1894*; Badamshin, 1949).

A comparison of the helminth fauna of the Caspian seal with that
of the northern seals (from which, according to some, the Caspian seal
has evolved) established that the Caspian seal "rid itself of almost all the
parasites characteristic of its northern kin but has become the host to
large numbers of two or three new species of parasites" (Dogel, 1947*;
Delyamure, 1955). Excluding the unidentified larval forms, 12 species
have been established among the helminth fauna of the Caspian seal
(Kurochkin, 1958, 1961,* 1962; Kurochkin and Zabolotskii, 1958; Delya-
mure, Kurochkin and A. Skryabin, 1964). From among the trematodes,
Criptocotyle lingua is a facultative parasite of the intestine; *Ciureana*
badamschini infects all the animals, with a few to half a million spec-
imens being found in the intestine of a single seal depending on the
severity of the infection; *Maritrema sobolevi* infects the intestine of 35%
of the seals with up to 300,000 specimens present when the attack is
severe; *Mesorchis advena* infects the intestine of 95% of the seals with up

to 300,000 specimens present in the case of severe invasion (Kurochkin, 1962); *Opisthorchis felineus*, a dangerous parasite of man and carnivorous mammals, infects the liver of 25% of the Caspian seals⁶³; and *Pseudamphistomum truncatum* infects the liver rather infrequently. Among the cestodes, *Ligula colymbi* is a facultative parasite of the stomach and *Diphyllbothrium phocarum* a parasite of the intestine. The nematode *Anisakis schupakovi* infects the stomach and is sometimes encountered among the seagulls but does not attain maturity in them. The larvae of this nematode infect almost all the fish found in the Caspian Sea (Kurochkin, 1961*), *Eustrongylides excisus* is detected in the small intestine, and *Parafilaroides caspicus* parasitizes the lungs of 20% of the seals with an invasion intensity of a few hundred specimens. The acanthocephalan *Corynosoma strumosum* infects the intestine of 70% of these seals (Kurochkin, 1962).

The helminth fauna of the Caspian seal offers justification to conclude that "the transition of the host to relict conditions of existence was marked, on the one hand, by a spurt in the speciation of parasites and, on the other, by a sharp modification of its parasite fauna" (Dogel', 1958). Thus the characteristics of the helminth fauna of the Caspian seal can serve as a reliable proof of the relict nature of this animal.⁶⁴

Specific data on diseases and epizooty are very scarce though it has long been known that a large number of seal carcasses, the so-called "plyvuns" or "plavurs," are annually washed ashore in the Caspian Sea in summer and autumn. The reason for such a loss of seals is not yet fully clear. An inspection of dozens of carcasses in November, 1957, did not reveal a single death that could be ascribed to helminth infection (Kurochkin and Zabolotskii, 1958). Probably, a considerable proportion of these floating bodies represents the wounded and killed animals that were not collected during the winter-spring hunting season (Chapskii, 1931; Badamshin, 1948; Kurochkin, 1958). The unfavorable ice conditions and storms which are particularly fatal to the young on ice floes play no mean role in natural mortality (Smirnov, 1931). At the same time, instances of the en masse death of seals during the second half

⁶³ "It could be said with certainty, for example, that a large independent focus of opisthorchiasis exists in the Caspian Sea. Suffering intensely from it during residence in the freshwater zone (especially in the prodelta), the seals spread the eggs of *O. felineus* with their excrement, thus infecting mollusks and later the fish through them" (Kurochkin, 1961*).

⁶⁴ It should be borne in mind that none of the three species of helminths that are common to the Caspian seal and the northern species "is specific to the pinnipeds". On the other hand, the species of parasitic worms characteristic of the northern seals, especially of *Phoca hispida*, are altogether absent in the helminth fauna of the Caspian seal. (K.Ch.)



216 Fig. 129. Caspian seal in open water pool. Gur'evsk Channel, February 1, 1966
(photograph by G. Nesterov).

of summer and in the autumn not only in the northern, but also in the southern and central Caspian, compel us to look for some other lethal factors. Pathological factors are also possible, including diplococcus which attacks not only the liver, lungs, and intestines, but also the muscles, joints, and skin. The percentage of diseases in some age groups is quite high (Vilezhanin,* 1965).

Population dynamics. The population dynamics of seals in the very early times when there was no hunting, in spite of the above factors (helminths and diseases), could hardly have been significant. After intense hunting began, it became the sole factor responsible for population fluctuations, in the background of which natural changes became imperceptible. It is also difficult to establish the effect of hunting since direct population data are not available. Indirect indices, primarily the extent of hunting, have to be relied upon (Badamshin, 1960, 1961).

The intensity of hunting in the first quarter of the nineteenth century (see below) was quite stable and prolonged at 150,000 - 160,000 animals (Sklabinskii, 1891) and this in itself points to the abundant population

of the animal at that time. However, some population reduction did occur even then judging from the reduced average number of animals killed annually, roughly at 110,000 - 120,000 in the next decade. This level of hunting continued right up to World War I. Evidently the population was still quite high and revealed 'no sharp drop although reduction nevertheless continued.

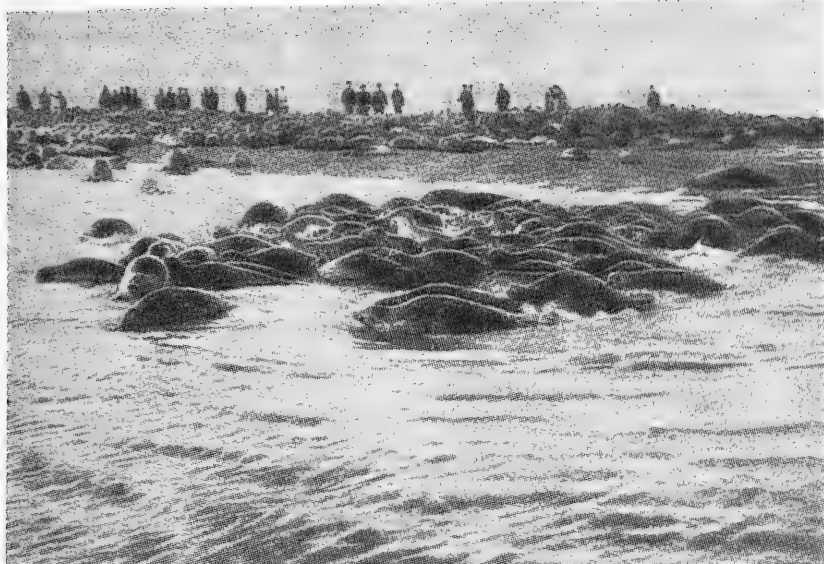
217 During the years of war, revolution, and civil war, Caspian seal hunting decreased markedly, the fall in population was arrested, and the herd multiplied. From the early 1920s, hunting recommenced and by the end of that decade had almost reached the prewar level, at which it remained until the mid-1930s. This restrained population growth and the herd began to dwindle in proportion to the intensity of hunting. Large-scale killing of the animals for several years in the 1930s severely affected the reserves (a maximum of 227,500 animals were killed in 1935). The high degree of hunting of mother seals and, concomitantly, pups, exerted a particularly adverse influence. The process of herd stabilization, although at a much lower level, was noticeable only in the 1940s while the population began to increase somewhat from the early 1950s (Badamshin, 1958*, 1960, 1961). However, by the mid-1960s, the Caspian seal population was far less than what it was more than a hundred years ago and this aspect has to be considered while planning the present-day hunting levels (see p. 289).

Field characteristics. Recognition of the Caspian seal from its external characteristics has never posed any difficulty since it is the only species of seal in the Caspian Sea (and in the lower courses of some rivers entering it). It is distinguished from the other species of the subgenus by color characteristics; the growing young and the adult sport innumerable spots of different shades, varying from gray (more rarely brown) to black in a light-colored general background; the clear spaces between the spots are usually not ring-shaped. (K.Ch.)

Economic Importance

As an important object of marine animal hunting, this seal occupies a foremost place in the number of seals caught in the USSR. Hunting (Fig. 130) has been practiced by the local coastal populations from very ancient times; the valuable raw material, i.e., hide, fur, and blubber, are used in various industries.

The antiquity of seal hunting is supported by references to the Caspian seal by Herodotus (N. Smirnov, 1931). The hunting of seals and partly the processing of raw material are of vital importance to the



218 Fig. 130. Autumn congregation of seals surrounded by hunters on the shelly shoals in the northeastern part of the Caspian Sea. October, 1958 (photograph by K.K. Chapskii).

economy of the Gur'evsk region of the Kazakh Soviet Socialist Republic and Dagestan Autonomous Soviet Socialist Republic.

During the first quarter of the nineteenth century, 150,000 - 160,000 animals were killed annually (Sklabinskii, 1891). In the next nearly 50 years (up to 1867), the annual catch varied around 105,000. The maximum number, 290,000, was caught in 1844. From the end of the 1860s to the beginning of World War I, an average of 115,000 seals were caught annually.

In the decade from 1927 through 1936, the average annual catch remained almost at the same level as in the prerevolution period, i.e., at 115,600 (Badamshin, 1960). At the end of the 1930s (1937 - 1940), it varied from 110,000 to 160,000, on average 147,500. In the 1940s, a much smaller number, 33,000 (1945) to 88,000 (1948), on average 64,400, were caught. In the 1950s, the hunting figures continued to drop: the average annual catch decreased to 47,000, ranging from 23,700 to 71,500; the average for the first half of the 1960s was 93,000 a year.

Until comparatively recently, the seals were caught in the Caspian mainly for their subcutaneous fat and hide, the latter mainly used as a raw material in the leather industry.

Among adult animals, during their maximum well-being (late autumn and winter immediately before whelping), the skin with blubber recovered by commercial methods (without flippers) weighs 40-50 kg, even 60-70 kg in some individuals. The thickness of the skin with the fat layer goes up to 7 cm at the breast level. In spring, however, after
 218 lactation and mating, and in recently molted animals, the weight of the blubber is reduced by half to 20 kg or less. A skin (without fat) weighs 3.5-4.0 kg. After summer fattening, toward autumn, the animals again recover spent reserves. Among the normally fattened and completely molted pups ("sivar"), the blubber weighs 10-13 kg and the skin alone without fat about 1.2 kg.

The seals are presently hunted for their fur and therefore only in the snowy period; the exclusive target is the newborn pup with a firm, furry white hair coat or a fully molted pup in which this wool is shed and a smooth and short fur has formed.

Wooden motor fishing boats with a load-carrying capacity of 35 to 40 tons are used for seal hunting. The aerial surveyor, who commences his work 2-3 weeks before the hunting season, plays a significant role. He usually arrives January end or early February. Additionally, 2-3 icebreaker-type vessels patrol the coasts and are available to those seeking assistance.

In the recent past, when the seals were mainly caught for their blubber and the fur was less coveted than at present, hunting continued almost year round. In winter hunting proceeded among the broken ice floes from fishing boats; when the ice floes became stable and firm, horses and sledges were used to reach the Gur'evsk Channel (from Dzhabbai village to the northern coast). Early in spring, when the ice thawed in the Volga, hunters set out in fishing boats and very small sail boats ("reyushkas") to kill seals molting on the drifting ice and icy hummocks. After the ice floes disappeared, island rookeries were raided and the animals caught together with sturgeons using fishing gear. At places (mainly
 219 in the region of Tyulen' archipelago), fishermen in oar boats hunted for the seals in water using firearms.

From spring until late autumn, hunting was carried out on the Apsheron archipelago islands; from September until total freezing, in the island rookeries in the northern Caspian; and from October through April, by using nets in the region west of Mangyshlak Peninsula. Females were the predominant targets.

To conserve the population, the hunting of adult females on ice floes was banned in 1966 and the killing of all seals except beleks and sivars was banned year round in 1967. Hunting of pups was restricted.

At present, although the total population has not yet been exactly ascertained, it does not exceed 500,000 and only a catch of 70,000 pups can be endorsed at the present time. Even this is an overestimate and in no way ensures the restoration of the population to its former maximum proportions.

With the prevailing state of the population, the number of animals killed should not exceed 40,000 a year (V.D. Rummyantsev).

Since 1973 aerial surveys have been undertaken of seals in the northern Caspian during the lactation period; such surveys will probably provide a new basis for an accurate census of the mothers and thus a rational ground for determining the hunting quota.

The adverse role of this seal as a killer of economic fishes has been discussed time and again. The reported instances of fish consumption, including white salmon, by these seals from fishing nets at various places (Varpakhovskii, 1891; Khlebtsov, 1902; and others) served as a basis for derogating this animal as an enemy of the fishing industry (Grimm, 1907; Averkov, 1914; and others). The general view thus created, consciously or otherwise, served as an extremely convenient rationale for unrestricted seal hunting, namely, destruction of a predator that killed large quantities of valuable commercial fish.

The objective data that has become available over time has helped to draw a more correct and complete picture, albeit not entirely comprehensive, of the food of seals, and also enabled a fresh assessment of their role in the fishing industry.

Even at the beginning of this century (N.A. Smirnov, 1907) it was found that items of very little commercial importance, especially goby, were very significant in the winter diet of seals. Subsequent observations (Dorofeev and Freiman, 1928; Roganov, 1930, 1931; Samofalov, 1931*; Terebenin, 1930; Badamshin, 1948, 1960) convincingly demonstrated that the Caspian seal was undeservedly branded an enemy of the fishing industry.

Even in years when the Caspian abounded in herring, Caspian roach, pike-perch, and others, not to mention the sturgeon, seals fed mainly on extremely low value and noncommercial fishes as well as invertebrates. Thus, in the spring of 1929, in the northern Caspian herring constituted only 14% of the food of the seal while the small Caspian roach and sabrefish played such an insignificant role that, together with the amphipods, they constituted only 2%; the seal subsisted mainly on sprat and to a small extent on sand smelt (Roganov, 1930).

Rearing these seals under artificial conditions has revealed their definite food selectivity. In all cases, when the seals had a wide choice of food items, they invariably preferred goby and sprat (Badamshin, 1948, 1960).

These seals have never had a predilection for the sturgeon. The reported damage by the Caspian seal to the fishing industry in the Caspian Sea is entirely baseless. Thus the Caspian seal is not responsible for the depletion of the Caspian fish reserves. (K.Ch.)

BAIKAL SEAL or BAIKAL RINGED SEAL⁶⁵

Phoca (Pusa) sibirica Gmelin, 1788

1788. *Phoca vitulina* var. *sibirica*. Gmelin. In: Linnaeus, Systema Naturae, Ed. XIII, I, p. 64. Lakes Baikal and Oron (the latter reference is erroneous).
 1872. *Phoca baicalensis*. Dybowski (Dybovskii). Izv. Sib. Otd. I. Russk. Geogr. Obshch., 3, no. 2, p. 86. Baikal.
 1922. *Phoca oronensis*. Dybowski (Dybovskii). Arch. Tow. Nauk. Lwow, I, p. 352, Nom. nudum. Lake Oron (there were never any seals in Oron). (V.H.)

Diagnosis

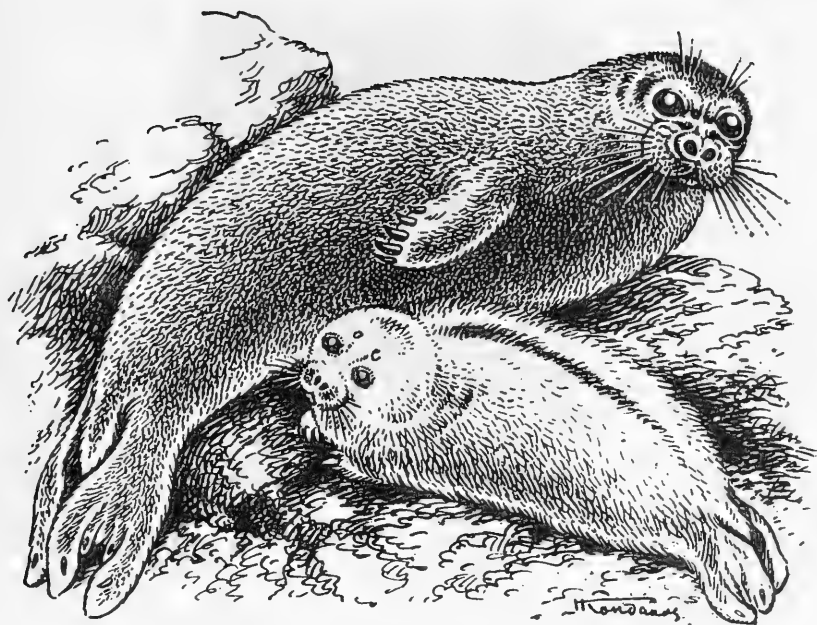
The color of the hair coat at all ages is monochromatic, without spots (Fig. 131). The fore flippers are totally covered by the hair; all the digits on the hind flippers are covered from outside, and only the two extreme ones are covered from inside. The claws on the fore flippers are long (up to 5 cm) and strong, and have a high triangular outline in cross section. The anterior edge of the nasal bones has no median projection.

Description

These seals are of small dimensions.

The hair coat is dense, short (up to 2 cm). The subcutaneous fat layer is thick (12 - 14 cm). The bones of the shoulder and forearm, and of the thigh and shank, are encased in a common skin cover. While moving, the forelimbs elongate to almost double their length due to the stretching of the forearm bones. The edge of the web extends beyond the tips of the claws of the hind flippers on which the longest digit is the first. The upper lip bears regular rows (usually eight) of 120 semi-transparent

⁶⁵ *Belyak*—white pup that has not shed the embryonic hair coat; *khubun* or *nerpyash*—molted underyearling; *chernysh*—one-, two-, and three-year-old seals; *yalovka*—unfertilized female; *matka*—gestating or whelping female; and *argal* or *sekach*—mature male.

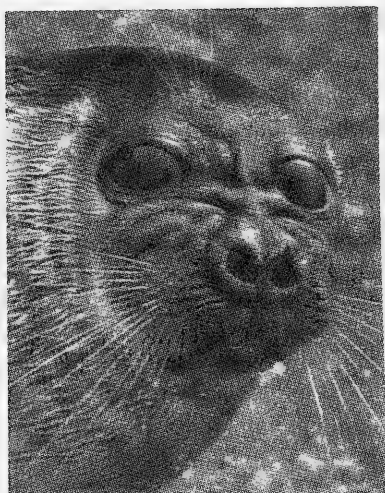


220 Fig. 131. Adult Baikal seal, *Phoca sibirica* (figure by N.N. Kondakov).



221 Fig. 132. Flippers with claws and cross section of claw of Baikal seal, *Phoca sibirica* (figure by N.N. Kondakov).

whiskers varying in length from 10 to 100 mm; the longest are seen at the corners of the mouth. The diameter of the eyeball may reach 47 mm (Figs. 133, 134).



221 Fig. 133. Head of adult male Baikal seal, *Phoca sibirica* (photograph by V.D. Pastukhov).



221 Fig. 134. Whiskers of the Baikal seal, *Phoca sibirica* (figure by N.N. Kondakov).

The color of the adults is silvery-gray dorsally, lighter on the flanks, and light gray, sometimes with an admixture of yellow, on the breast and belly (especially in the arm pits). Age-related color variations are not significant. Spottiness is seen as an extremely rare exception.

The skull is thin-walled; the zygomatic width is much more than the mastoid width and considerably more than one-half the condylobasal length (Fig. 135). The zygomatic arches are distinctly seen when the skull is viewed from behind. The anterior edge of the nasal bones forms only two lateral processes. The posterior edge of the bony palate is usually in the form of braces (Fig. 136). The tympanic bullae are not large and the gap between them is usually equal to the length of each. The interorbital space is narrow, not more than 4 mm in adults. The molars and premolars have additional cusps, set without gaps; their accessory cusps extend roughly parallel to the main one. The teeth in the upper jaw are



Fig. 135. Skull of the Baikal seal, *Phoca sibirica* (figure by N.N. Kondakov).

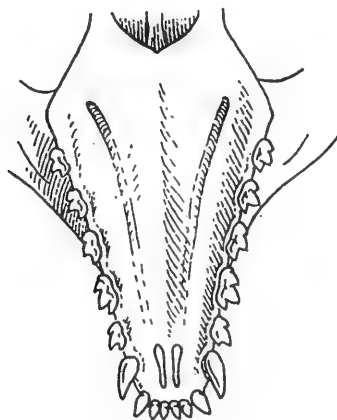


Fig. 136. Bony palate of the Baikal seal (figure by N.N. Kondakov).

usually more spaced than the lower ones (Ognev, 1935; Ivanov, 1938; Chapskii, 1955, 1963) (Fig. 137). The body length from tip of nose to tip of tail is 110-142 cm in a straight line. The



Fig. 137. Teeth of the Baikal seal, anterior view (figure by N.N. Kondakov).

largest male measured was 141 cm long and the female 142 cm. The length differences between sexes is insignificant. The weight of the adults is 45-55 kg but some individual animals can reach 100 kg. The weight of the blubber is 25-29 kg. The internal organs weigh (g) on average: heart 300-400 (heart index 6.66-7.27), liver 900-1400, lungs 400-500, kidneys 300, spleen 400, stomach 600, and intestine 400.

The condylobasal length of the skull is 173.5-204.4 mm, width at zygoma 108.3-121.2 mm, and maximum width of skull 95.8-102.9 mm (Ivanov, 1938). Age-related changes in the structure of the skull are as follows.

1. The cranial capsule of the young seal is relatively larger than that of an aged seal. Measured from the posterior edge of the orbits (along the posterior edge of the interorbital constriction) to the posterior edge of the occipital bone, its length is roughly equal to the entire remaining half of the skull, from the posterior edge of the orbit to the anterior section of the intermaxillary bones. Among adults, the length of the cranial capsule is roughly equal to the distance from the posterior edge of the orbits to the end of the nasals.

2. The central portion of the nasal bones among young seals is considerably wider than in adults. The width of these bones is usually noticeably more than the longitudinal diameter of the alveolus of each of the upper canines.

- 223 3. The bony lobes of the lower outer edges of the auditory meatus among young seals are relatively wider than in adults (Ognev, 1935).

A small number of seals of very small dimensions, some with predominantly ochreous shades, have been encountered. It is suggested that these do not represent individual variations but "starvelings," i.e., pups which have lost their mothers in the period of lactation but yet somehow managed to survive; they are termed dwarfs (Ivanov, 1938). (V.A.)

Taxonomy

The Baikal seal represents an independent advanced species of a group that is well adapted to living in fresh water.

In craniological features the Baikal seal is closely related to the Caspian but its evolution is evidently not directly related to the latter. There are two hypotheses of the evolution of the Baikal seal: its entry into the Baikal during the Quaternary along the rivers of Yenisey-Angarsk or the Lena system from the Polar Basin, and the arrival of the ancestors of this seal in the pre-Quaternary period from the Sarmatsk-Pontichesk Basin. The first of these hypotheses is more widely accepted and has been confirmed by fairly weighty arguments from helminthologists. The louse parasitizing the Baikal seal belongs to the species *Echinophthirius horridus*, found on the seals of the northern seas, while the nematode, *Contracaecum osculatum*, detected in the Baikal seal is a widely distributed parasite of the seals inhabiting polar waters. Evidently the view of the northern origin of the Baikal seal is more correct (Ass, 1935; Mozgovoi and Ryzhikov, 1950; Chapskii, 1963; Lomakin, 1964). (V.A.)

Geographic Distribution

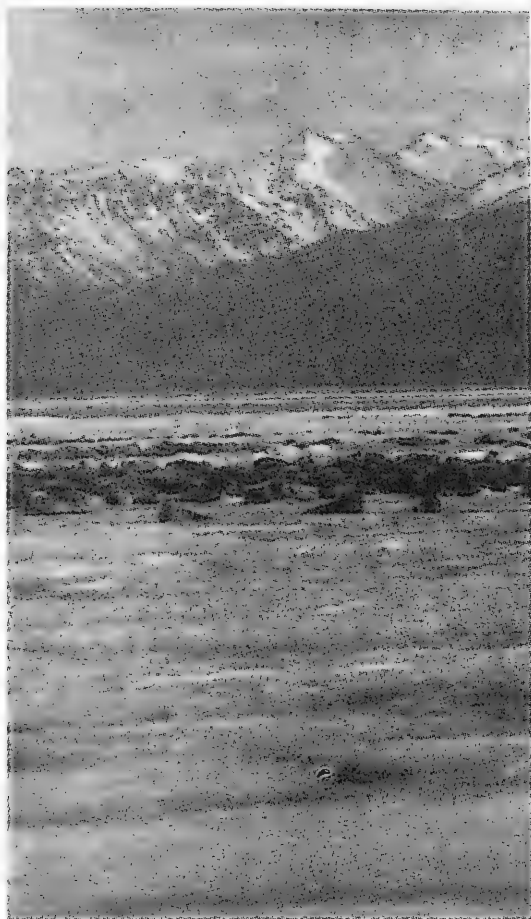
These seals are not found outside the boundaries of Lake Baikal. They inhabit mostly the northern half of the lake where extremely significant beach rookeries are formed in the summer months. In winter they are distributed more uniformly, but are fewer in the southern half of the lake (Ivanov, 1938; Pastukhov, 1961). (V.A.)

Geographic Variation

Not reported. (V.A.)

Biology

Population. In the spring of 1953, an aerial survey was made of the seals resting on ice floes and of their air holes. The data recorded for the surveyed sections were extrapolated to the entire area of the lake, taking into account the density of disposition of the animals. The total population was thus determined at 20,000-25,000 (Sviridov, 1954). On the basis of a census of the seals on ice floes in autumn in the main regions of the concentration of the animal together with the assumed number of seals in the other (less important) sites of autumn concentrations, the



224 Fig. 138. Haunt of seals on the ice. Northern Baikal (photograph by V.D. Pastukhov).

population later was put at 35,000-40,000 (Pastukhov, 1967). All these figures should be regarded as approximate.

Habitat. In the winter months the seals inhabit mainly floating ice under a continuous ice sheet, using air holes in the hummocky ice floes for respiration. From the time of thawing of the ice floes to their total disappearance, the animals form rookeries on the ice (Fig. 138). In summer and autumn, beach rookeries are found mainly on the northeastern coast of St. Nos and Ushkan' Islands in the south. Some "extinct" (Ivanov, 1938) rookeries which were regularly inhabited

sometime in the past, are seen in the southern part of the Baikal. The summer rookeries are distributed on the coastal flat stones jutting out of the water, slightly away from the coast.

Food. Examination of the stomach and intestinal tract of some 500 seals provided information about their food for almost the entire year in different parts of the Baikal (Pastukhov, 1965b, 1967). Most of the stomachs of the Baikal seal investigated were found to be empty, which is characteristic of the other species of Pinnipedia too. Semidigested food remains were detected only in three stomachs but the intestine and especially the rectum invariably contained the remnants that were difficult to digest (otoliths; eye lenses, etc.). These provided a basis for identifying the species of fishes consumed (Table 13).

In addition to the 17 species of fishes listed in Table 13, the food of the Baikal seal included some species of invertebrates: gammarids of the genera *Odontogammarus*, *Macrochectopus branickii* (pelagic), *Garjajewia* (deep water), and *Acanthogammarus*. Mollusks of the genus *Baicalia* were detected twice. Sand, pebbles, and mica were found quite often in the alimentary canal.

Table 13. Species composition of fishes consumed by the Baikal seal (Pastukhov, 1956b)

Species of fish	No. of seals in which this species was detected	Frequency, %
Baikal omul, <i>Coregonus autumnalis migratorius</i> Georgi	8	6.6
Stone sculpin, <i>Paracottus kneri</i> Dyb.	3	2.5
Sand sculpin, <i>P. kessleri</i> Dyb.	22	18.0
Big-headed sculpin, <i>Batrachocottus baicalensis</i> Dyb.	3	2.5
Spotfin Baikal sculpin, <i>B. multiradiatus</i> Berg.	4	3.3
Yellowfin Baikal sculpin, <i>Cottomephorus grewigki</i> Dyb.	70	57.4
Longfin Baikal sculpin, <i>C. inermis</i> Jakowl.	70	57.4
Red Baikal sculpin, <i>Procottus jettelesi</i> Dyb.	9	7.4
Humped sculpin, <i>Asprocottus megalops</i> Gratzian	2	1.6
Big red Baikal sculpin, <i>Procottus jettelesi major</i> Tal.	1	0.8
Big Baikal oil-fish (big golomanka), <i>Comephorus baicalensis</i> Pall.	60	49.2
Lesser Baikal oil-fish (lesser golomanka), <i>C. dybowskii</i> Korotn.	92	75.4
Common perch, <i>Perca fluviatilis</i> L.	5	4.1
Burbot, <i>Lota lota</i> L.	2	1.6
Ide, <i>Leuciscus idus</i> L.	1	0.8
Siberian dace, <i>Leuciscus leuciscus baicalensis</i> Dyb.	1	0.8
Roach, <i>Rutilus rutilus</i> Pall.	6	4.9

Throughout the spring and summer the food of the seal evidently remains the same and is restricted mainly to four species of fish: yellowfin Baikal sculpin, longfin Baikal sculpin, big Baikal oil-fish, and lesser Baikal oil-fish. "Other species of sculpin" occupy a very insignificant position. The autumn food of the seal is somewhat more diverse though the number of predominantly consumed fish species even at this time does not exceed eight. The list of fishes consumed by the seal in winter is similarly restricted to four species. Some food differences are seen in different regions of Baikal but since the list of food items itself is small, the differences too are not large.

Gammarids were found in the stomach of most of the seals in the year of their birth. The seals take to fish with advancing age. There are no other convincing data on age-related food variations.

225 The number of commercial fishes consumed by the Baikal seal (mainly in the autumn) is so insignificant that this animal cannot be regarded as a threat to the Baikal fishing industry. The main food consists of the Baikal oil-fish and goby, which are of little use to man (Pastukhov, 1965b).

Home range. The Baikal seals have distinct home ranges only in the winter since most of them live close to air holes at this time (Fig. 139). Barren females, immature seals of both sexes, and adult males live singly around one or several air holes; the animals sometimes use common air holes. The females and the newborn during lactation have their own home ranges among caves under the snow.

Hideouts and shelters. Holes in the ice floe can be regarded as such structures only by stretching the interpretation. The simplest of them are the air holes of barren females, adult males, and immature seals. These are in the form of a cone enlarging downward and ending in a small opening at the top. When making the air holes, the seals quite often
226 take advantage of the natural openings formed during the hummocking of ice floes and keep them open throughout the winter. In other cases the animal has to make such holes by breaking the ice when it is still thin or even "biting" it with their teeth and scratching it with their claws.

The nesting holes of the female represent genuine shelters. They consist of a large opening 40-80 cm in diameter in an ice floe through which the female can freely emerge from the water and the lair. The latter is made in the snowdrifts adjoining the hummocks and is invariably on the leeward side of the prevailing winds. The lair is in the form of a snow cave with its arch and walls covered with an ice crust formed by the respiration of the animals. The ice cover imparts adequate strength to the cave. The smallest of the lairs measured was 47 cm high, 110 cm long, and 108 cm wide (Ivanov, 1938). Some were much larger. Sometimes the



225 Fig. 139. Air hole in an ice floe made by an adult male Baikal seal (photograph by V.D. Pastukhov).

roof of the lair thaws and an air hole is formed. The female undergoes parturition in the lair and suckles the pup; molting of the juvenile hair coat of the pup is probably completed in the lair also.

Daily activity and behavior. Data on these aspects are extremely scant. In winter, from the moment of ice formation, most of the seals spend continuous time in water, rising in the air holes only for respiration; hence it is impossible to study their behavior.

From early April the seals form spring rookeries on the snow. The first to arrive are the immature animals (one-, two-, and three-year-olds). Sometimes some mature males are also seen among them. The en masse emergence of pups on the ice occurs in mid-April, at which time the changeover from suckling to independent feeding takes place. The next to arrive are the barren females and adult males, followed finally by mothers that have undergone parturition in the current year.

The seals bask in the sun in different postures: on the back, sideways, and on the belly. A characteristic posture of nearly all the animals of every age is the head turned toward the air hole and in its immediate proximity. Initially the animals are extremely restless and rapidly "disappear" in the water at the slightest hint of danger. A "reassured" animal is quieter but often raises its head and may suddenly disappear in the water at any moment.

The summer rookeries are almost exclusively colonized by the females. The animal population in the rookery changes round the clock somewhat systematically. The seals are usually not found in the rookery until 7:00 a.m. They start approaching from 7:00-8:00 a.m. and arrive in the lair at 8:00-9:00 a.m. Later, the number of seals increases gradually and reaches maximum by 11:00 a.m. The number then begins to decrease and approaches minimum by 1:00-2:00 p.m., but once again increases by 3:00 to 4:00 pm. Maximum numbers are seen at 6:00 p.m. but by 8:00 to 9:00 p.m. the rookery is almost empty. The periodic departures of the seals for feeding explain these population variations in the rookery (Ivanov, 1938).

In spring the seals feed more intensively at night and in the early hours of the day (the stomach of seals caught toward evening never contained food remnants while only some caught in the morning had an empty stomach). The period of intensive feeding exhibits seasonal variations (Pastukhov, 1965b).

Seasonal migrations and transgressions. The Baikal seals perform regular but relatively small migrations in the Baikal water body. Whelped and barren females and part of the mature males pass the winter on the eastern coasts while the immature seals and part of the adult males do so on the western coasts. Early in spring large ("polyn'yas") air holes are formed in the ice at the same places every year along the eastern and western shores of the Baikal. The first of the spring rookeries of seals are formed along these shores. With the formation of a large number of
227 fissures and tears close to the western shore, a large number of mature males and barren females migrate there from the eastern shores and, as a result, fairly large congregations of seals are formed at times on the western shores.

At the end of May, in the southern half of the lake, the ice begins to break up and floating ice floes are gradually carried northward by the prevailing southwestern winds. Along with these drifting ice floes, almost the entire southern herd of seals reaches the north and forms numerous rookeries there on them. Beach rookeries are formed after the ice floes thaw. Only a small number of seals, regarded as "locals", remain in the southern part of the lake.

The beach rookeries begin to break up early in autumn. The seals finally abandon them by September-October and concentrate on the eastern shore of the lake in Proval, Barguzinsk, and Chivyrkuisk bays, and in the estuarine sections of the Upper Angara, i.e., along much of the eastern shore. Such rookeries are not seen only in the extreme southeastern part of the shore. All of these shallow-water regions are protected from the autumn winds and hence covered with ice floes earlier than in other zones. As soon as the shore ice is strong enough to support the weight of the animals, the seals form sometimes fairly large (hundreds of animals) rookeries on it. Animals of both sexes and of different age groups are seen in the rookeries, which remain in force for 1.5 to 3 months depending on the time of total freezing.

As the ice zone enlarges in the shallow-water regions, the seals hold onto its edges and gradually move toward the unfrozen deeper part of the lake; not a single animal remains in the shallow-water zone in November-December (period of total freezing). The edge of the ice zone, running comparatively close to the eastern shore, is regularly split by wind and waves and the broken floes enter the open Baikal carrying the seals with them. Here the animals no longer form large groups but divide into small ones spread over a large area. From the time of the final freezing of the lake, the seals take to living under the ice until the lake opens up in May. Spring hunting is concentrated mainly in these regions (Ivanov, 1938; Pastukhov, 1961). Thus the Baikal seal performs regular though short-distance seasonal migrations.

Some stray transgressions of the Baikal seal occur in the rivers entering or emerging from the Baikal, Salenga to Selenzhinsk (280 km) and even up to Ust'-Kyakhty (400 km), Barguzin to Ust'-Barguzin, and downward along Angara to Irkutsk (not exactly) and up to Olonka village (150 km) (Ivanov, 1938; Lomakin, 1964).

Reproduction. No direct observations of the mating of the Baikal seal have been reported. Presumably, mating occurs in water under the ice cover at March end to the first half of April, soon after the birth of pups (Pastukhov, 1966). Most of the females undergo parturition in February and March and only some stray births occur earlier or later. Even at the beginning of April, females in the last stages of gestation or newborn pups (with the umbilical cord not yet dry) are very rare. Thus the pups are born while the females are still on stationary ice floes. Usually, the female undergoes parturition in a snow cave (see above). The entire duration of whelping extends for 30-40 days.

A study of the embryos and an analysis of the sex ratio of the seals caught showed that the male to female ratio is close to 1:1 (Ivanov, 1938).

A study of the female genitalia revealed that the period of sexual maturity and reproductive capability extends to several years. At the age of 2-5 years (from the state of the genitalia), the females become potentially mature but do not actually participate in reproduction. At the age of 3-6 years they attain productive maturity and the first fertilization has been observed among the four-to-seven-year-old females. All the seven-year-olds and older females investigated were already mothers. Later, they whelp almost every year since barrenness affects only 12% of them. Gestation extends for 11 months, of which the first three represent the latent period of fetal growth (Pastukhov, 1966, 1969a).

Growth, development, and molt. The pups of the Baikal seal are very large at birth and measure one-half the length of the mother (Fig. 140). Lactation extends for 2-2.5 months and the pups grow very rapidly. Of the eight pups weighed in April (1-1.5 months after birth), the smallest weighed 22 kg and the largest 44 kg; average weight 31.3 kg (Ivanov, 1938).

The newborn pup is covered with a dense yellowish-white hair coat 3-4 cm long. In 1.5-2 months, quite often even during the period of residence in ice caves, i.e., from February end to early April, the embryonic hair coat is completely shed and the pup acquires the color of the adult (Fig. 141). The molting period of the adults is considerably prolonged



Fig. 140. Newborn Baikal seal pup (photograph by V.D. Pastukhov).

and its duration depends to some extent on the well-being of the animal. Some seals begin to molt even in early May. At May end and in early June, the number of molting seals is already significant but molting animals may be encountered throughout June and even up to mid-August. It is assumed that the better fed the herd in a given year, the earlier the onset of molt; the faster molt proceeds, the sooner it is completed (Ivanov, 1938).

Enemies, diseases, parasites, mortality, and competitors. This herd suffers the most damage from bears, which prowl the beach rookeries. There are no other enemies.

Among the ectoparasites, the louse *Echinophthirius horridus* (Olfers, 1816) Fahrenholz, also known among other true seals, Steller's sea lion, and fur seals, has been reported on the skin of these seals. This parasite of the Baikal seal has been isolated as a distinct subspecies, *E. horridus* var. *baicalensis* Ass.

The helminth fauna is represented by a single species of nematode, *Contracaecum osculatatum* (Rud., 1802) Baylis. A distinct subspecies of this species, *C. o. baicalensis* Mosgovoy and Ryjikov (Ass, 1936; Delyamure, 1955), is present among Baikal seals.

The diseases and causes of mortality of the Baikal seal have not been studied. Probably, some seals perish every year in winter due to unfavourable conditions of the Baikal ice crust.



Fig. 141. Molted pups of the Baikal seal (underyearlings); unmolted pup seen in the foreground (photograph by V.D. Pastukhov).

Population dynamics. Noticeable natural changes in the population of the Baikal seal have not been reported. The population varies only in relation to the hunting activity. Further, the number of seals caught also reflects to some extent the variation in their total population. Although the total catch rose sometimes to 9,000-10,000 per annum in the pre-revolution years, hunting activity subsequently decreased. It again rose in the 1930s when the total catch reached 6,000-6,500 per year. In subsequent years, catches steadily decreased, which is explained by a reduction in total population. This downward trend continued and the catch never exceeded 1,500 per annum. The population dynamics were strikingly dependent on hunting, which ultimately led to a significant reduction of the entire seal population (Pastukhov, 1965a).

Field characteristics. The Baikal seal is characterized by a monochromatic fur free of spots. It may be further noted that no other species of seals exists in the Baikal region. (V.A.)

Economic Importance

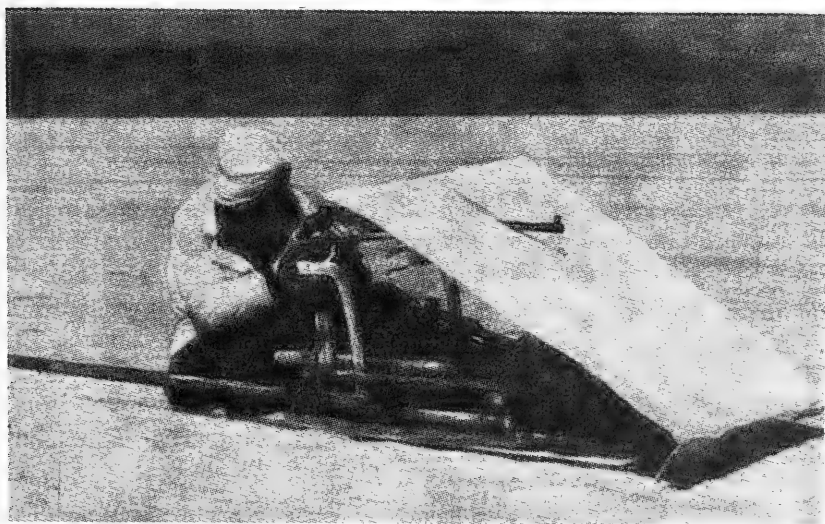
Hunting data in the pre-revolution period are scant and contradictory; the annual catch of seals has been put at 3,500 to 9,000-10,000 by various authorities. Evidently the significant proportion of the catch fully utilized by the hunters themselves has not always been included in catch records. At the end of the 1920s, the annual catch was 3,500-4,000 seals. Commencing from 1931, the volume of hunting rose and comprised an average of 5,700 for six years (maximum 6,466); later hunting gradually declined. From 1940 through 1950, the average annual catch was 1,484 seals but fell to a mere 847 from 1950 through 1960. The annual catch
230 in this period never exceeded 1,500 seals. It should be borne in mind that a certain quantum of catch does not always figure in the accounts as it is used privately; this figure in some years could be almost equal to the official figure. The actual annual catch [in this decade] was about 2,000 (Pastukhov, 1967, 1969b).

The Baikal seal is of no importance except to the local people for whom its hunting plays a growing role with increased production of raw furs.

The technique of catching these seals is as typical as it is diverse. Formerly, hunting was carried out year round but experience showed that successful hunting on the spring ice floes accounted for almost all of the annual catch. Therefore, from 1935, hunting in the summer and autumn beach rookeries was banned and later, hunting in the southern half of the Baikal was also prohibited. These measures did not reduce the annual kill. Subsequently, hunting from boats was banned. Thereafter,

hunting on sledges became the main method and the hunting season declared open from April 25. A group of some 20 hunters with horses harnessed to sledges set up a hunting camp on a Baikal ice floe. Usually each hunter has his own horse-drawn sledge but sometimes two hunters use the same sledge. Early in the morning, the hunters set out in different directions in search of the seals. On sighting resting seals through binoculars, the hunters leave their horses 2-2.5 km away from the animals. Then, sporting little white caps and pushing their small sledges adorned with white sails in front of them, the hunters endeavor to approach as close as possible to the seals (Fig. 142). The sail has two openings, one for observation and the other for shooting through. Concealment against the sun and invariably against the wind is also necessary as otherwise a seal can sense a hunter's presence far beyond the shooting range.

The Baikal seal is so sensitive that, even under favorable conditions, it is impossible to approach it within less than a hundred meters. Having come within the required range, the hunter shoots the seal with a rifle and then runs headlong toward it with a hook since even a mortally injured animal can, with its dying breath, still dive into the water; the hunter has to catch it on the ice. In a successful hunt the horse sledge
 231 is brought to the kill, the seal loaded on it, and the chase for the next animal begun. The hunters return to camp in the evening with one or two and sometimes even as many as ten seals.



230 Fig. 142. Device for concealment from seals. Baikal (photograph by V.D. Pastukhov).

When the ice is thin and dangerous for sledges, the hunters set out on foot, which greatly reduces the hunting range. However, even when using sledges, some hunters operate on foot (Ivanov, 1938).

Hunting by means of boats (now banned) used to commence after the ice floes had broken up. The hunters negotiated the channels using small boats with the prow masked by a white sail. On sighting an animal, the hunter turned the boat toward it so that the vessel remained concealed behind the sail. The animal was shot with a rifle, the kill loaded on the boat, and brought to the camp in the evening, where all the hunters gathered.

In recent years, hunting by sledges has undergone some mechanization. In the 1960s, hunting on foot almost ceased and most of the hunters chased the seals on horseback but some began using light motorcycles for towing the hunting sledges. Finally, in 1969, any type of hunting of the adult animal was totally banned. At present, the use of rifles is permitted on the spring ice from April 25 for shooting seals only below the age of one year.

Much effort has been expended in the preservation and restoration of the population of the Baikal seal. Gradually, hunting in the summer, autumn, and winter, and in the southern half of Lake Baikal, as well as of all adult animals was prohibited. Finally, a norm was fixed for the annual kill. The most effective measure has been the banning of killing of adults and allowing the catch of only pups.

Hunting of unmolted pups in snow caves, where they shed the embryonic pelage, is practically impossible. It is therefore recommended that hunting of molted underyearlings be permitted. These are far bigger than the unmolted pups (average weight 20 kg and weight of blubber 12 kg) and provide a no less valuable fur. Shooting with rifles could then be totally prohibited as this results in inevitable losses in the form of injured animals and damaged fur. The young seals should be caught in nets laid under the ice. The right time for catching them in this manner is the end of April (not before April 25) since by then all the pups have molted and lactation has ceased. Test catching in nets has shown that adults are not trapped in them (Pastukhov, 1967, 1969b).

At the present level of population, the annual kill can be set in the range of 2,000-3,000 with no loss to the herd (approved limit 2,500). This change in the system of utilizing the herd can promote its population rise. The organization of census work can provide a base for rational regulation of hunting. A catch of young "fur-bearing" animals is far more economical than hunting for "skinny" adults. (V.A.)

Subgenus of True Seals
Subgenus *Phoca* Linnaeus, 1758

COMMON SEAL, LARGA⁶⁶
***Phoca (Phoca) vitulina* Linnaeus, 1758**

1758. *Phoca vitulina*. Linnaeus. Syst. Nat. Ed. X, 1:38. Northern part of the Baltic Sea.
- 232 1811. *Phoca largha*. Pallas. Zoogr. Rosso-Asiatica, 113. Eastern coast of Kamchatka.
1811. *Phoca canina*. Pallas. Zoogr. Rosso-Asiatica, 1:114. Atlantic (?).
1820. *Phoca variagata*. Nilsson. Skand. Fauna, 1:359. Atlantic (?).
1823. *Phoca scopulicola*. Thienemann. Reise im Norden Europas, 1:59. Iceland.
1824. *Phoca littorea*. Thienemann. *Ibid.* Northern Russia (?).
1828. *Phoca linnaei*. Lesson. Diction. classique d'Histoire Natur., 13:415. European waters.
1828. *Phoca thienemannii*. Lesson. *Ibid.*, 13:414. New name for *Phoca scopulicola* Thienem.
1828. *Phoca chorisii*. Lesson. *Ibid.*, 13:417. Kamchatka.
1844. *Phoca nummularis*. Temminck. Fauna Japon, p. 3. Japan.⁶⁷
1864. *Halicyon richardii*. Gray. Proc. Zoolog. Soc. Lond., p. 28. Vancouver Island.
1902. *Phoca ochotensis*. J. Allen. Bull. Amer. Mus. Nat. Hist., 16:480. Gizhiga Estuary, Sea of Okhotsk. Nec *Phoca ochotensis* Pallas, 1811.
1902. *Phoca ochotensis macrodens*. J. Allen. *Ibid.*, 16, p. 483. Avachinsk Bay, Kamchatka.
1902. *Phoca steinegeri*. J. Allen. *Ibid.*, 16, p. 485. Commander Islands (Bering Island).
1902. *Phoca richardi pribilofensis*. J. Allen. *Ibid.*, 16, p. 495. St. Paul Island, Pribilof Islands.
1936. *Phoca vitulina largha natio pallasii*. S. Naumov and N. Smirnov. Tr. Vses. n-i. in-ta rybnogo khozyaistva i okeanografii (VNIRO), 3:177. Sea of Okhotsk.
1941. *Phoca petersi*. Mohr. Zoolog. Anzeiger, 133, p. 49. Coasts of the Korean Peninsula.

⁶⁶ Also mottled seal (Far East), rock seal (sometimes in Murman).

⁶⁷ According to King (1961), this form has been described by Temminck from material of the ringed seal, *Phoca (Pusa) hispida* Schreb., and hence should be excluded from the synonyms of *Phoca (Phoca) vitulina*.

1942. *Phoca ochotensis kurilensis*. Jnukai. Shokobutsu Dobutsu, 10, no. 10, p. 930. Southern Kuril Islands.
 1964. *Phoca insularis*. Belkin. Dokl. AN SSSR, 158, no. 5, p. 1217. Iturup Islands (Kuril Islands) Cape Dokuchaev. (V.H.)

Diagnosis

The *larga* is a large, well-proportioned seal. The body length measured along the dorsal surface (*Lc*) exceeds 1.5 m; the neck and the snout are somewhat elongated. The color of the hair coat varies from a bright mottled and contrasting (with a predominance of light-colored background, speckled with small gray and black spots) to intensely dark color with clear spaces in the form of oval rings or streaks (Fig. 143).

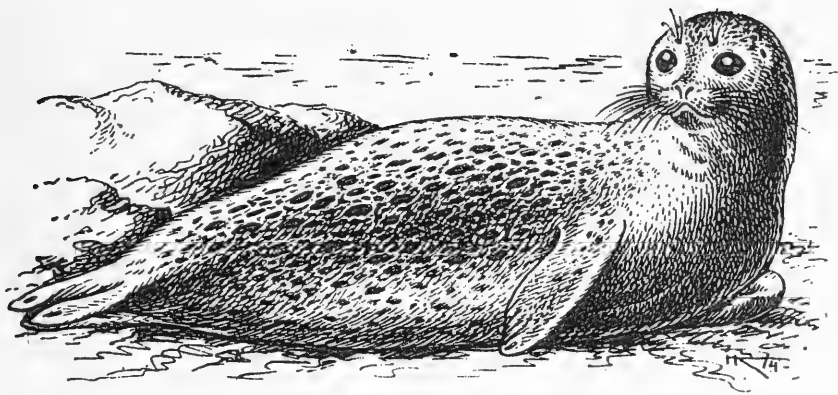
The skull is relatively massive and its length not less than 190 mm; the interorbital width usually exceeds at least 1.5 times, and the total width of the nasal bones at the base of their apex (along the frontal-maxillary suture) at least two times the smallest diameter of the sub-orbital aperture. The longitudinal width of the crown of the second to the fourth upper premolars usually exceeds the height of the crown. The accessory cusps of the corresponding lower teeth are short, usually less wide-set, and close to the main cusp as though adjoining it (Fig. 144). (K.Ch.)

Description⁶⁸

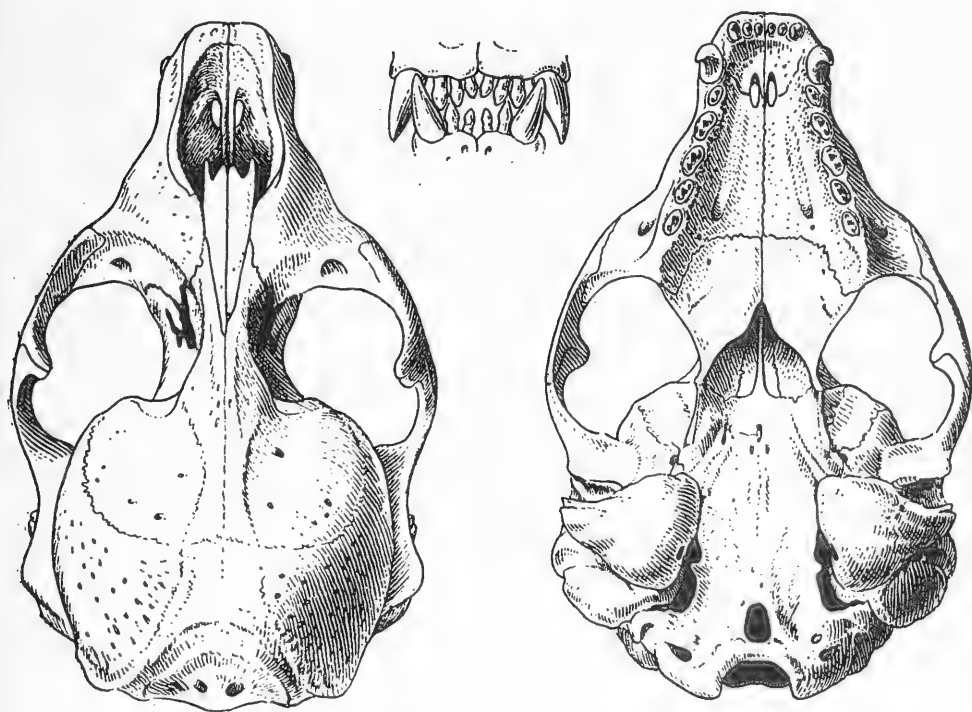
In terms of body proportions, the seals of this species can be regarded as typical of the genus. The fore flippers are relatively small, somewhat shorter than the hind flippers. The third digit on the fore flippers together with its claw is shorter than the second and the first while the second is often somewhat longer than the first or equal to it. The whiskers are fairly well flattened, with wavy edges, and set in six rows (only one whisker in the seventh row) with the maximum number (8 or 9) in the second and third rows from below; the total number of whiskers on each side of the snout varies from 39 to 48. The supraorbital whiskers number five each, rarely four each; one whisker each occurs near the nostrils. The nares are bordered by a narrow strip of bare skin.

The color of the hair coat after the first (infantile) molt exhibits extreme variation not only individually, but also in relation to the

⁶⁸ The *larga* described here is the arctic Far Eastern form (for more details, see "Geographic Variation").



233 Fig. 143. Common seal, *Phoca v. vitulina*. Atlantic Ocean (figure by N.N. Kondakov).



235 Fig. 144. Skull of the common seal, *Phoca v. vitulina* (figure by N.N. Kondakov).

geographic distribution of the population and its affinity to the pagophilic or pagophobic group.

These seals can be divided into two main types—very dark and very light-colored. The dark type is most often encountered in the group of Atlantic common seals and also among the pagophobic⁶⁹ populations of the Pacific Ocean part of the range. The light-colored type is common among the pagophilic Pacific populations, i.e., the *larga*.

Among the dark-colored animals, the main background is either very highly pigmented or very densely covered with additional, very large spots. One way or the other, there is little space for the light-colored sections on the dorsal side of the body. Such sections are seen sometimes only in the form of narrow and sinuous light-colored streaks, more often as short, as if broken streaks in the form of light-colored dabs on a dark-colored background or as indistinct rings. Dark-colored animals are also encountered with large contrasting rings and an abundance of minute ringlets interspersed with spots of diverse shapes, sizes, and colors (usually with an indistinct contour and often superposed on each other). These are colored different shades of brown-olive, cinnamon, dark gray, and black. The ventral side of such specimens is also usually dark-colored although the color of the spots on it is somewhat fainter (see Plate III).

The main color of the light-colored animals, on the contrary, forms a light-colored background on which dark gray spots admixed with black ones are scattered quite densely. The black spots appear as though superposed on the dark gray spots and rarely as dabs. This significant diversity of color acquires a very definite and distinct character in the background of geographic variation (see pp. 323–330).

The age-related color changes have not been adequately traced (Millais, 1904; Havinga, 1933; and others) due to extensive individual variation of all the elements constituting the skin pattern. Among the under-yearlings of the European common seal, a broad, dark, and more monochromatic (brownish) band extends along the middle of the back from the head to the tail. This band is only slightly interrupted by dark-colored specks and gaps which are usually smaller than those among older animals. This is also a characteristic of the Pacific Ocean forms, including the *larga*. The ventral side is silvery-white, with extremely rare spots in most cases. Sometimes, however, even young animals are encountered with innumerable spots on the belly, as noticed among the pagophobic form (Fisher, 1952) and the arctic *larga* (Chapskii, 1967). The spots on the body flanks are more diverse in number, brightness, and configuration. The color of the head is lighter than among older animals.

⁶⁹ Breeding not associated with ice floes.



Plate III.

Island or Kuril seal, *Phoca (Phoca) vitulina kurilensis* Inukai, and largha, *Phoca (Phoca) vitulina largha* Pall. (in the rear) (figure by N. N. Kondakov).

With age, the dark-colored dorsal band gradually becomes mottled with white gaps, often in the form of fairly distinct oval rings. As a result, the median longitudinal band on the back, which is distinctly monochromatic among juveniles, ultimately disappears altogether. Further, such a process of age-related color changes is evidently not seen among all underyearlings. Animals are encountered among them (Moore, 1955*; Heinroth, 1956*; and others), which are almost indistinguishable from the adults either in differences in mottled clear spaces medially on the back, or in the development of innumerable light-colored oval rings on the dorsal side of the body, or in the color of the head.

Young animals, which have yet to reach adult size, are generally similar in color to the latter but nevertheless differ in a more monochromatic color of the back (Ognev, 1935). Fully adult and older animals have a more vivid and contrasting spottiness in which the dark and light components of coloration are fairly evenly represented and uniformly alternated, creating a bright mottled, speckled pattern usually lost on the light-colored ventral side. This is relevant, however, only to a definite type of spottiness that is especially characteristic of the Atlantic forms and the arctic *larga*. Coloration is highly diverse and very light-colored animals are also encountered together with brightly mottled and very dark, sometimes almost wholly black animals. The dry skin of the light-colored animals appears almost white from a distance.

The hair coat of the under-yearlings is softer, somewhat denser, with a better developed "layer" of thin, tender, and extremely short hairs, almost like underfur. The coat of adults is considerably coarser; the setaceous guard hair (base of the coat) is thicker and dominates sharply over the underfur, which is difficult to distinguish among this coarse guard hair (Havinga, 1933; Fisher, 1952).

The color differences between males and females have not been thoroughly distinguished; some regard the spotted pattern as more intensely manifest among males (Havinga, 1933); others (Millais, 1904) consider the back of the female to have more dark spots while the ventral side is covered less densely with spots than in the male and the color of females is therefore considerably paler. The ringed pattern is better developed among male *largas* than in females and the color in general is brighter and the pattern better contrasted (Chapskii, 1967).

Information on the seasonal color variation requires verification. It was pointed out (Millais, 1914*) that before every molt the general color shade, as well as the intensity of spots, turns much lighter and duller as though faded. According to other authors (Havinga, 1933), the color of the hair coat turns a dirty yellow before molt.

Two main types are noticed in the structure of the skull (Fig. 144) as also in the color of the hair coat. These types are associated with the ecological and taxonomic grouping of the species into two forms as pagophilic and pagophobic.⁷⁰ Among the animals of the pagophobic form represented in the Atlantic Ocean, the nasal processes of the maxillary bones usually do not reach the nasal bones or sometimes only slightly contact the latter without wedging deeply posteriorly between their outer edge and the maxillae. The length of the anterior part (rostrum) of the nasal bones in most cases somewhat exceeds one-half their total length. The uncinat processes of the pterygoid bones are in the form of club-shaped thickenings or hooks slightly flattened laterally and not bent outwardly. The bony nasal septum in the choanae does not extend posteriorly farther than the anterior edge of the palatine bones. The posterior edge of the bony palate is distinctly notched, often with slightly curved sides and usually with an additional angular notch medially. The occipital foramen [foramen magnum] usually has a high angular notch on the upper edge. The premolars, except the first, are large; the second and the third, with rare exceptions, are disposed obliquely in relation to the tooth row in such a way that the anterior edge of the last tooth runs somewhat inward beyond the posterior edge of the preceding tooth. The anterior articular edge of the zygomatic bones is somewhat longer than the total of their posterior edge measured between the most prominent points.

The body length of adult seals⁷¹ caught on the Dutch coasts and measured in a straight line (L_{cv}) was around 150 cm in most cases, the largest of them reaching 160-165 cm⁷² (Havinga, 1933). The maximum length evidently not measured in a straight line, but along the dorsal surface (L_c) among the Norwegian seals is 180 cm (Collett, 1911-1912). On the German coasts the length of the largest animals (measured evidently along the dorsal curvature) does not exceed 175 cm (Moore, 1955*).

According to one view in the literature, the Pacific Ocean seals of this species are larger than their Atlantic counterparts (N. Smirnov, 1929; Ognev, 1935; Bobrinskii, 1944*, 1965*). Such an assumption, however, is justified only on an indiscriminate comparison with the latter of all

⁷⁰ The skull description is based on specimens from the North and Barents seas (nominal form). For the skull characteristics of the Far Eastern form, see under "Geographic Variation".

⁷¹ Various authors cite the sizes of seals in their own way and do not always clearly state how the animal was measured—in a straight line or along the dorsal body curvature.

⁷² The values cited by Havinga expressing the body length along a straight line but up to the tip of the hind flippers have been converted using his own conversion factor (13%).

the seals belonging to the various Pacific Ocean forms, although their taxonomic structure is quite varied. In fact, the pagophobic seals of the Far East, for example from the Kuril Islands, are perceptibly larger: the body length (L_c) of the largest animals is around 200 cm or even more (Belkin, 1964). The larga, however, belongs to the pagophilic forms and its maximum dimensions are no different from those of the Atlantic seal at maximum length (L_c) 175 cm (S. Naumov, 1941) to 182 cm (Chapskii, 1967).

Under the conditions of intense oppression by man, the small size of the European seal is perhaps wholly to be expected; at the same time, natural factors too could have been responsible for the size differences.⁷³

The length of the adult male larga averages 173 cm (L_c), of the female 162 cm. Two very large female adults caught on the southern coast of the North Sea weighed 76 and 105 kg; the maximum weight of two males was 100 and 114 kg (Moore, 1955*). Two male Okhotsk largas in the spring weighed 92.5 and 96 kg while an adult female also caught there weighed 82.5 kg (Wilke, 1954); the weight of male Bering largas in the spring reached 100 kg and that of females 88 kg.

The condylobasal length of the skull of adult animals of both sexes from various parts of the range varies from 190 to 255 mm. Among adult males, the skull on average is 10 mm longer than that of adult females. The width at the zygomatic arches exceeds the width at the mastoids: among adult largas, the former measured 110-138 mm and the latter 112-125 mm; the rostral width varied from 31-45 mm.

The relative weight indices of the internal organs among male largas in the spring at an average body weight of 73.5 kg are as follows: heart average 6.3%, lungs (with trachea and larynx) 13.3%, liver 26.2%, kidney 2%, and stomach 9.2%. (Sokolov, Kosygin and Tikhomirov, 1966). The length of the os penis among adults is 13.5-14.0 cm (for more detailed body and skull dimensions, see "Geographic Variation"). (K.Ch.)

Taxonomy

The seals of the subgenus *Phoca* are usually compared with those of the subgenus *Pusa*, and especially with the ringed seal (*Phoca hispida*), from which they have inherited many features. However, the structure of the cheek teeth reveals significant differences and these along with

⁷³ Data on the Atlantic seals are extremely scant and fragmentary and there is no accurate information on their actual ages. Moreover, the oldest and the largest rarely attract hunters.

some other differences probably justify the placement of these species in different but nevertheless very close genera.

The taxonomic structure of this species in its broader interpretation, as adopted in this publication, has been reviewed several times and even today evidently cannot be regarded as conclusively established. In spite of describing several forms from the Pacific Ocean (see under synonyms), its taxonomic structure in the waters of the USSR has long led to two subspecies: Atlantic—*Phoca v. vitulina* L. and Pacific—*Phoca v. largha* Pall. (N. Smirnov, 1929; Ognev, 1935). However, the ecological population and morphological heterogeneity of the Pacific population of the common seal (Chapskii, 1960) detected after the 1930s necessitated a review (see p. 158). As a result, the efforts of researchers attempting to reflect the diversity of the Pacific Ocean seals by describing new species and subspecies had to be evaluated from a new viewpoint. Of particular interest at present are the attempts of Allen (1902) who described a new species of seals from the Commander Islands (*Ph. steinegeri*) and Inukai (1942) who pointed out that it be regarded as a special subspecies of the larga (*Phoca kurilensis*). This tendency again intensified in the 1960s following the collection of extensive new data on the ecology, morphology, and distribution of the Pacific Ocean seals. As a result, suggestions were made to regard the Kuril "island" seal (Belkin, 1964; McLaren, 1966) and the pagophilic form of the larga (Chapskii, 1966, 1967; McLaren, 1966) as independent species.

It is possible to interpret differently the ranks of these seals but the following premises in any case are beyond doubt. Firstly, the Pacific Ocean members of the subgenus *Phoca* s. str. cannot be regarded as a single form whatever the level be, species or subspecies, assigned to it. The ecological and morphological features of the larga are so sharp that they run beyond the limits of even the so-called good subspecies. Secondly, there is greater relative similarity between all the pagophobic populations of the Pacific and Atlantic than between the Pacific Ocean forms of different ecological types (i.e., between the pagophilic larga on the one hand and the pagophobic, island or Kuril, seals, and Richard's seal on the other). As a result, the species of the common seal, *Phoca vitulina*, according to some authors (Chapskii, 1966a, b, 1967; McLaren, 1966) should be divided into two species: 1) common seal—*Phoca vitulina* L., and 2) larga—*Phoca largha* Pall. The composition of the second species (larga) thus does not include the pagophobic Pacific seals, possibly deserving in turn the rank of an independent species. In the present work, however, according to the note on p. 158 and the general attempt to resist extreme division of the species, the larga has not been regarded as an independent species. (K.Ch.)

Geographic Distribution

This includes the waters of the continental shelf of the temperate and subarctic belts of the Atlantic and Pacific oceans with the congruent limited regions of the North Arctic Ocean. The overall range, interrupted by the arctic seas and land fringes of Asia and America is distinctly divided into two isolated sections: North Atlantic and North Pacific. These represent a typical example of interrupted amphiboreal distribution.

Geographic Range in the USSR

Commensurate with the above character of overall distribution, the seals belonging to this group inhabit, on the one hand, our western marine boundaries and, on the other, the Far East (Fig. 145).

On the western coasts of the USSR the Atlantic seal is encountered almost only in the Murman region in the east up to the inlet and in rare cases up to the isthmus of the White Sea. It is not found in the central basin and the White Sea bays. In the middle of the last century (Ber, 1862*), it was reported in Novaya Zemlya but no one found it there subsequently.

In our territorial waters of the Baltic, the distribution has not been established with certainty either on the southwestern continental coasts of the Estonian Soviet Socialist Republic, on the Khiuma and Sarema islands (Aul, Ling, and Paaver, 1957), or in the coastal waters of the Latvian and Lithuanian Soviet Socialist Republics. References to the rather frequent encounter of this seal on the Baltic coasts including even Estonia (Lewis, 1885*; Grosse and Transehe, 1929) should be regarded as erroneous. In general the correct view of the distribution of the common seal in the Baltic Sea was established even in the 1930s, when it was regarded as an inhabitant of only the western and southern fringes of the sea (Freund, 1933). However, in the adjoining parts of the sea, especially in Gdan'sk Bay, the common seal was without doubt encountered in the recent past (Ropelewskii, 1952). Its incidental find therefore is wholly possible on the coasts of Kaliningrad region although it may not be a regular inhabitant there. Its presence even more northward along the Lithuanian and the adjoining sections of the Latvian coasts is also possible. There is no doubt of its absence in the Gulf of Finland.

Thus in the USSR waters of the Atlantic portion of the range the seals of this species are distributed almost exclusively at places where there is no formation whatsoever of a stable ice crust. This pattern of distribution wholly corresponds to the ecological nature of the European

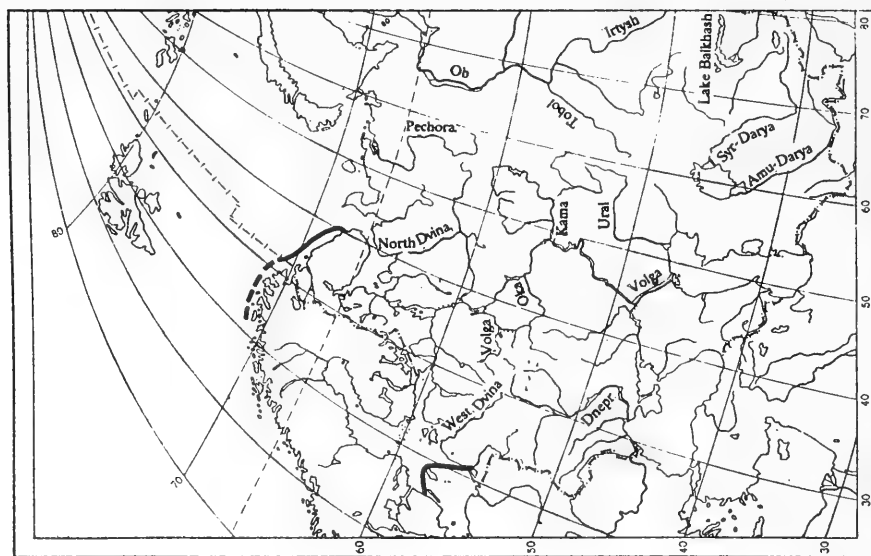
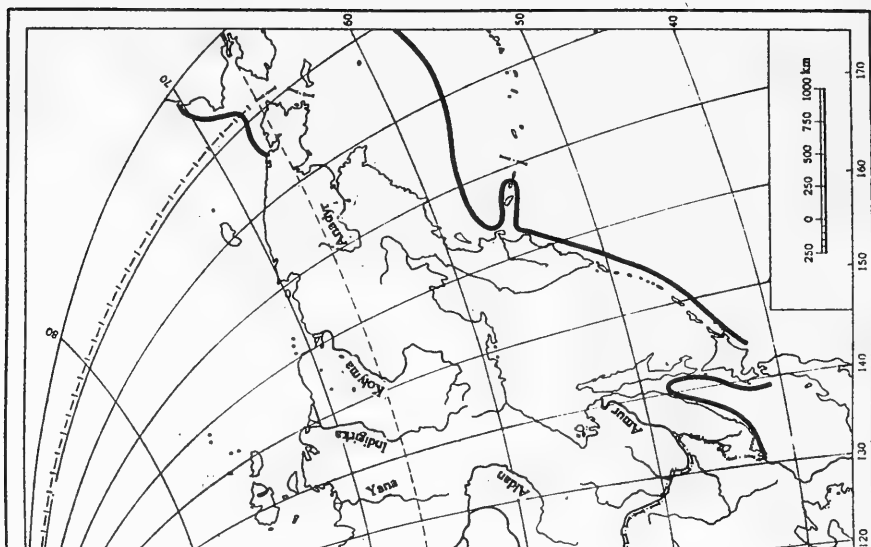


Fig. 145. Distribution of the common seal, *Phoca vitulina*, in the USSR (K.K. Chapskii).

populations of the species pertaining to the pagophobic form though some animals and groups can be encountered on ice floes.⁷⁴

In the USSR waters of the Far East the seal, essentially belonging to a different ecological-taxonomic (pagophilic) form, is distributed very widely from the USSR boundary with the People's Democratic Republic of Korea to the coasts of the Chukchi Peninsula and the southernmost part of the Chukchi Sea adjoining the Bering Strait.⁷⁵ In the Sea of Japan the *larga*⁷⁶ is common in the Peter the Great Gulf and is encountered north of it along the coast up to Tatar Strait where its concentrations are considerable on the continental coasts, Sakhalin coasts, and on the ice floes away from the coasts.

In the Sea of Okhotsk this seal is distributed all along its periphery but unevenly and not uniformly in different seasons. In spite of adaptation to breeding on ice floes, in winter the *larga* does not remain close to the continental coasts and islands surrounded by dense, massive, generally stationary ice floes, but prefers instead the more pelagic regions of the sea with drifting ice floes abounding in many pools of open water and washed-out holes. The main regions in which the *larga* is concentrated in the snowy period of the year in the Sea of Okhotsk, according to the latest data (Fedoseev, 1970; G.A. Fedoseev) are: the western part of the sea (opposite the mid-northern part of Sakhalin Island and also in Terpeniya Bay), northwestern coast of Kamchatka, in Yamsk and Tauisk Bays, and in the region from Cape P'yagina to the Kola Peninsula. In summer, with the thawing of ice floes, the entire population of the Okhotsk *larga* is wholly concentrated in the coastal belt of the sea. The animals are not dispersed uniformly all over the territory, however, but gather mostly in the regions that provide the most favorable food conditions. The estuarine sections of innumerable rivers are extensively used and the *larga* transgresses quite far from the estuary into many such rivers. The uneven distribution becomes even more perceptible closer to autumn as a result of seasonal concentrations of the population in certain fixed sites year after year where coastal rookeries are formed. They are concentrated in three very important regions: (1) in the western part of the sea (Shantarsk Islands), (2) in its northeastern fringe (including Shelikhov Gulf and Taigonos Peninsula), and (3) in the coastal belt of

⁷⁴ Three specimens of this species were caught in such an environment on the Murman coasts, between Kil'din Island and Nokuev Bay, in the spring of 1901 (Smirnov, 1903).

⁷⁵ The *larga* hardly spreads along the polar coast of Eastern Siberia into the west beyond L'ong Strait although there are references (Rutilevskii, 1962) that it perhaps reaches even the estuary of the Indigirka River.

⁷⁶ For accurate definitions of "*larga*" and "Kuril or island seal," see under "Geographic Variation".

western Kamchatka. In the first of these zones rookeries are formed on the mainland coast where they are generally few, as well as on the islands.

240 In the western part of the Gulf of Sakhalin small rookeries and stray haunts are encountered on individual reefs of Capes Litke and Mofet (S. Naumov, 1941). Some rookeries are seen in Konstantin Bay (western-most corner of Akademii Bay). A rookery exists in Nikolai Bay. The existence of rookeries has not been confirmed in Ul'bansk Bay although the larga is found there in autumn. In Tugursk Bay rookeries are known in Mamga and Kumchai bays and also near the isthmus separating Tugursk Bay from Konstantin Bay. In the Shantarsk archipelago rookeries are found exclusively on the small islands: Sivuch'i Kamni (northern and southern), Utichii, Ptichii, Srednii, and on the reefs close to Bol'shoi Shantar Island (Pikharev, 1941; S. Naumov, 1941).

In the region of Taigonos Peninsula, where the larga is preferentially confined in summer to the estuary sections of the more southern rivers of Penzhinsk and Gizhiginsk gulfs, beach rookeries were noticed in the early 1930s mainly in the proximity of Capes Verkholamsk, Naklonnyi, Krainii, Povorotnyi, and Pupyr'; on Tretii and Krainii, Khalpili, Rechnaya Matuga, and Uikana islands; and also in Taigonos and Dorozh'ya bays. Farther to the southwest, the larga was similarly distributed all over the region and its rookeries were found in the same places year after year, the most important of which are Cape Ostrovnyaya, estuarine sections of the Berezovka and Ireta rivers, and several points on the P'yagina and Kona peninsulas (Freiman, 1936).

In Tauisk Bay rookeries were found mainly in Motyklei, Tokhar', and Stanyukovich bays, and on Nedorazumeniya Island; they were also seen in Nagaeva Bay and on the open coast from it to Kholkhotlya (Freiman, 1936). In the early 1960s, rookeries in Tauisk Bay were seen on Capes Polonsk and Amakhtonsk, in Melkovodnoi Bay, and at some other places (Tikhomirov, 1966). Recently, Babushkina, Ushki, Shel'tinga, and Penzhinsk bays, and also sections on the western coast of Kamchatka have also been cited (G.A. Fedoseev).

In the Tigil'sk region of western Kamchatka, right in the early 1930s, rookeries were detected (Lun', 1936) at 10 places on the coast: (1) 20-25 km north of Lesnaya River, (2) 10-13 km more to the north, (3) on Cape Kinkil'sk, (4) 40-50 km north of Amashino River, (5) on Cape Babushkina, (6) on Tal'nichnaya Islet (15 to 20 km south of Cape Babushkina), (7) near Moroshechnaya River, (8) near Cape Utkholoksk (Kavachinsk rookery), (9) on Cape Yuzhnyi (Utkholoksk rookery), and (10) in the other Moroshchechnaya River (south of Cape Khar'yuzov) (Lun', 1936).

Six rookeries were detected in 1958 roughly in the same section of the western Kamchatka coast: two in the lower courses of Moroshchechnaya River, one on Cape Khar'yuzovo, one on Cape Yuzhnyi, and the rest near Cape Utkholoksk and Cape Babushkina (Tikhomirov, 1966a).

No definite data whatsoever are available on the concentrations of larga on the continental coast of the Sea of Okhotsk to the southwest of Okhotsk; however, as at other places, here too the larga is found in the summer-autumn season but more isolatedly, and evidently without forming regular rookeries.

On Sakhalin, it is common not only along the western coast, especially in the northern part commencing roughly from the threshold of Nevel'sk Strait to the Gulf of Sakhalin inclusive (Tyk Strait, Cape Lak, etc.; Gakichko, 1931), but also on the eastern side. In the northern third of Sakhalin largas are confined in larger numbers than in the more southern regions, on the open beaches as well as in Nyisk, Daga, Chaivo bays, and are particularly abundant in Pil'tun Bay, forming here and there fairly regular rookeries (Ambroz, 1931).

The Kuril range is inhabited almost wholly but the true larga inhabits mainly the northern and southern islands, being almost wholly absent in the central part of the range inhabited by the pagophobic island or Kuril seal, which is more widely distributed there, on no less than 28 islands including the Malaya Kuril range (Belkin, 1964; Marakov, 1968).

241 The coastal strips of the southern half of Kamchatka, western as well as eastern, fall in the normal range of the larga; the island seal, however, inhabits predominantly the sea coast. Both forms are encountered on the Commander Islands, predominantly on Mednyi Island in Zabobrovaya and Zapalata bays in the northwestern extremity (Marakov,* 1966) forming regular rookeries there. The majority represent the pagophobic form of seal; the larga is encountered there comparatively rarely.

The summer-autumn rookeries on the coasts of southern Kamchatka are generally few. They are noticed particularly near the estuary of the Mutnaya River, on Capes Khodzhelaika and Senyavina, and also in the region of Vakhil' River; about a hundred seals were counted in each area (Ostroumov, 1966). In Karaginsk Gulf, the larga is common and even abundant at times in winter and summer and there is even a rookery along the coasts of Karaginsk Island (N.N. Gerasimov). The animals inhabit other points too, including Avachinsk Bay (V.F. Muzhchinkin). Groups of them are found in the region of Kronotsk Bay from July through October in the estuarine sections of the Kronotskaya, Tikhaya, and Mutnaya rivers (in water as well as on sandy shoals) (R.M. Viktorovskii). The range in the Bering Sea encompasses the entire coastal

belt from Kamchatka to the Bering Strait. The larga is evidently encountered almost exclusively (arctic form of the subgenus) in all of this extensive expanse, covering the region of Parapol'sk Dolo and Karaginsk Island, Olyutorsk Gulf, Koryak coast, and Gulf of Anadyr, as well as the Chukchi Peninsula coast. This coastal zone is unfavorable to the habitation of the island pagophobic seal as it is blocked by the winter ice floes with the exception of only the southernmost part; this very factor is responsible for the seasonal distribution of the larga. As in the Sea of Okhotsk, it is confined here in winter to the areas far away from the coasts in the sea beyond the limits of the shore ice and highly cohesive but broken ice practically outside the continental zone. Only at places along the Chukchi Peninsula coast where the shore ice is not much and open pools are formed, is it seen there from time to time even in winter, thus providing a basis for affirming that it is confined there year round (Freiman, 1936b).

In the winter-spring season the range of the larga in the northern part of the Bering Sea enlarges roughly up to the edges of drifting ice floes whose disposition is unstable. The range can extend even beyond the limits of the continental shelf by the time of maximum ice floe formation. The main collections of the larga at this time are seen along the extensive edges of the ice floes (at some distance from the very fringe deep onto the ice floes), in the region of St. Matthew Island in the northeastern part of the sea, and almost up to the Pribilov Islands. Another part of the population at this time is usually found in the zone of drifting ice floes in the Gulf of Anadyr.

With spring thawing of the ice floes and also to some extent with the movement of their masses under the influence of the prevailing southeastern current, the "pelagic" part of the range gradually recedes northward and by June end (when ice floe remnants are seen only in the northwestern corner of the Gulf of Anadyr) is confined to a narrow strip fringing the contour of the mainland. In this summer-autumn period isolated stray sections of the range inhabited temporarily by small local populations are formed around the St. Lawrence, St. Matthew, and Pribilov islands. This situation, however, is extremely hypothetical.

On the southern Chukchi coasts, although rare, the larga is encountered everywhere. In the Chukchi Sea west of the Bering Strait, distribution of the larga extends in the form of a small tongue into the coastal belt, evidently only to Kolyuchinsk Bay (P.G. Nikulin; Tikhomirov, 1966b), which thus represents the western arctic boundary of the Pacific Ocean part of the range (see footnote on p. 317).

243 *Geographic Range outside the USSR*

Coasts of Japan, Korean Peninsula, and China up to the Yangtse. In the territorial waters of the Korean People's Democratic Republic and South Korea, some stray or a few animals are seen here and there, and probably not every year; they penetrate on the west coast up to Yonilman Bay (Nishiwaki and Nagasaki, 1960)⁷⁷ (Fig. 146).

On the Japanese coasts the large is more common on Hokkaido Island. It is carried on drifting ice to the Okhotsk coast and the pagophobic form enters from the Kuril Islands. It is also encountered on the Pacific Ocean side and on the coasts of the Sea of Japan. Evidently it transgresses south of Sangarsk Strait, along the coast of Honshu Island and up to Cape Inubo and possibly even more southward (Nishiwaki and Nagasaki, 1960). The range for the western side of this island has been shown in extremely general terms (Moore, 1965*). Sometimes the animal enters even up to Kyushu and Osumi islands.

Young animals are seldom seen every year in spring on the Chinese coasts of the Yellow Sea (on Shantung Peninsula) (Leroi, 1940*; Schaffer, 1958). Yet the seals enter even the Yangtse estuary (Allen, 1938).

On the American side of the Pacific Ocean and the Chukchi Sea the seal is distributed along the entire coast from the northern Alaskan coasts through the Bering Strait and the eastern coastal section of the Bering Sea (including the Aleutian Islands). It then extends in a narrow belt all along the Pacific Ocean coast including the Alexander archipelago, and south to the Californian Peninsula (Mexico) at 28° 12' N lat. (Cedros Island).

Along the northern coast of Alaska the seal reaches east beyond Point Barrow, entering the estuary of the Colville River (Bee and Hall, 1956) although it is extremely rare there; it was noticed even on Herschell Island (near the estuary of the McKenzie River).

In the European part of the northern Atlantic it extends to the extreme southwestern regions of the Baltic Sea (along the Swedish coasts in the north not farther than Gotland Island), in the Denmark Strait, and the adjoining regions of the North Sea. From here, one branch of the range extends north and northeast along the Norwegian coasts up to Murman; another branch runs along the western side of Jutland, along the coasts of the Federal Republic of Germany and Holland up to Pa-de-Kale. Here the range branches again: the smaller and weaker

⁷⁷ The authors undoubtedly committed an error by assuming that the ringed seal (*Phoca hispida*) inhabits within the boundaries outlined by them. Equally erroneously, they point to the distribution of this species in the south and along the eastern coast of Honshu Island.

branch runs along the French coasts, encircles Brittany, and is lost in Biscay Bay. Rarely, stray animals sometimes reach the Spanish coasts and extremely rarely even the Portuguese coasts (41° N lat.). In the north, from La Manche, the range includes the coastal waters of the British Isles and Ireland and also the west and north of Scotland: Hebrides archipelago, Orkney, Shetland, and Feeroe islands. The coastal waters of Iceland represent an isolated section of the Atlantic part of the range; here the common seal is distributed almost everywhere and is regarded as the most abundant representative of the *Pinnipedia* (Semundsson, 1939*). Along the eastern coastal waters of Greenland, the range extends north up to the Polar Circle and along its western coasts moves roughly up to 73° N lat. up to Upernavik (Mansfield, 1967) although some stray animals are encountered from time to time even more northward (Vibe, 1950).

The American part of the North Atlantic range mainly encompasses the Canadian coastal waters north of Mann Strait including Nova Scotia, Gulf of St. Lawrence, Newfoundland Island, and the Labrador coast. Farther north and west, the seal is distributed along the eastern, southern, and southwestern coasts of Baffin Island and along the entire coast of Hudson Bay. Lancaster Strait can be regarded as the westernmost point of records of this seal in the Canadian archipelago (Mansfield, 1967).

South of Canada, along the eastern coast of the United States, it is encountered rarely and only some stray animals reach the state of North Carolina at times. (K.Ch.)

Geographic Variation

Early in this century concepts regarding the species and subspecies of seals of the subgenus *Phoca* s. str. were quite confusing because of the extremely incomplete descriptions that were often difficult to compare. At least three species and three subspecies belonging to the same subgenus were proposed for the Pacific part of the range alone (Allen, 1902). Later, attempts to recognize the infraspecific differences (N. Smirnov, 1908; Ognev, 1935; S. Naumov and N. Smirnov, 1936) tended to return to the viewpoint of Nordquist (1882*), according to whom the subgenus has only one species, *Ph. vitulina*, and only one subspecies, *Ph. v. largha*, vicariating with the European *Ph. v. vitulina*, which inhabit the entire Pacific Ocean Basin.

Even the latest revision of the seals of the genus (subgenus) *Phoca* adopted by Doult (1942) did not alter the prevailing situation. Moreover, Doult affirmed that he was not able to detect any characteristics which could distinguish the animals on the American coast of the northern part

of the Pacific Ocean from their counterparts on the Asian coast. It was equally impossible to distinguish the Atlantic European common seals from the American seals.

Doubt notwithstanding, differences between some populations of the Pacific and Atlantic members of the subgenus *Phoca* were once again confirmed while concomitantly the differences noticed within the Pacific populations remained unexplained (Chapskii, 1955). With further study of the systematics of the latter, the reason for the heterogeneity of the Pacific populations of the subgenus was found in their ecological differences (Chapskii, 1960). With the growing collection of specimens and greater information, the taxonomic heterogeneity was demonstrated more fully (Belkin, 1964; Moore, 1965*; Chapskii, 1965, 1966, 1967; McLaren, 1966). It was possible to differentiate these seals into two groups based on ecological as well as morphological features: pagophilic seals breeding on ice floes and aigialoid or pagophobic seals breeding on land.

According to some contemporary scientists (McLaren, 1966; Chapskii, 1966, 1967), who assign an independent species status to *Phoca largha* Pall., the *largha* is almost the only form belonging to the first group of pagophilic seals. Seals of the second group, of which five forms have been described, wholly represent a different proximate species, *Phoca vitulina* L. As pointed out above, in this publication the *largha* has been regarded as a subspecies.

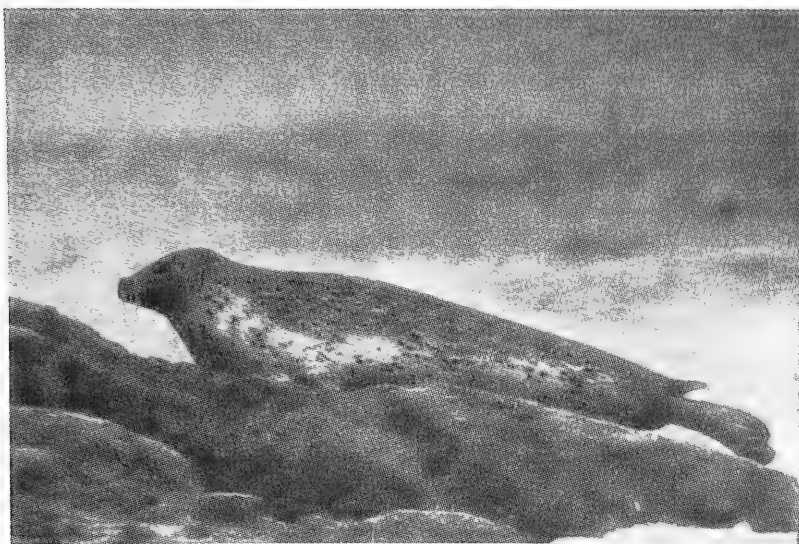
Three subspecies of one or the other types are encountered in Soviet waters. In general, however, the geographic variation of the common seals in our waters has not yet been adequately studied.

1. Larga, mottled seal, *Phoca (Phoca) vitulina largha* Pallas, 1811 (syns. *ochotensis*, *macrodens*, *pallasii*, *petersi*).

Body length (along the dorsal curvature, *Lc*) varies from 150 - 180 cm and condylobasal length of the skull, 185 - 230 mm.

The color (Fig. 147) is relatively light, mottled: the main background on the underside of the body is whitish, light silver, while the upper part is mostly dark with a fairly dense network of rather small whitish oval streaks or rings and with small but vividly colored spots (brownish to black) scattered over the body. The newborn sports a white furry coat that lasts through the lactation period.

The transverse profile of the tympanic bullae reveals a steep and high drop to the base of the shortened and rounded lobe of the external auditory meatus (Fig. 90). The less stable skull features are as follows: the nasal processes of the maxillaries extend far posteriorly along the nasal bones, while the frontal part of the nasal bones is shorter than one-half their total length (Fig. 92); the posterior edge of the zygomatic bone has



245 Fig. 147. Typical coloration of an adult pagophilic large, *Ph. v. largha*. Verkhovurov Island, Kuril range, August, 1971 (photograph by S.V. Marakov).

245 an arcuate notch (Fig. 91); the bony nasal septum in the choanae runs posteriorly beyond the anterior edge of the palatine bones to the middle and farther than the latter; the posterior edge of the bony palate has an oval outline or even an additional arcuate notch at the center, and the uncinat processes are usually flattened and turned outward (Fig. 93); all the premolars are located directly one behind the other and not inclined relative to the general line of the tooth row.

This subspecies inhabits the Far Eastern seas from Peter the Great Gulf and Pos'et Bay to the limits of the range in the Chukchi Sea, including Tatar Strait, Sea of Okhotsk, northern and southern islands of the Kuril range, the Bering Sea, and partly the Commander Islands.

Outside the USSR it is found in the coastal waters of Alaska (in the Chukchi Sea in the east to the limits of its range), Aleutian, Pribilov and other islands in the eastern part of the Bering Sea, south to Bristol Bay. South of the USSR border, it is found up to the northern coasts of Japan and the Yellow Sea inclusive.

Two races (natio) were identified within this form (S. Naumov and N. Smirnov, 1936). One of them, *n. pallasii*, distributed in the Sea of Okhotsk and in the northern part of the Sea of Japan, is a very small form according to S. Naumov and N. Smirnov (condylobasal length 188-228 mm). The other race, *n. largha*, inhabiting the Bering Sea,

differs from the preceding one in much larger craniometric dimensions (condylobasal length 191-238 mm). The differences between these races are artificial since the Bering *larga*, according to the above, represents a mixture of the typical *larga* with the pagophobic populations (Kuril or island seal). It is possible that the Okhotsk *largas* in fact are somewhat smaller than the Bering counterparts and differ from them in other features, but they should be compared exclusively with the pagophilic kin. These "races" are not consistent in the proposed form.

2. European common seal, *Phoca (Phoca) v. vitulina* Linnaeus, 1758 (syns. *canina*, *variegata*, *scopulicola*, *littorea*, *limnaei*, *thienemannii*).

Does not differ much from the *larga* in size. The body length (along the dorsal curvature, *Lc*) varies from 175-180 cm; the condylobasal length of the skull of adult males varies from 203-217 mm and that of females 190-205 mm, average 205 mm (Ognev, 1935).

- 246 The color is more or less dark. The main background on the upper side is dark, quite often almost black, interrupted by white, uneven cellular streaks; the underside is lighter; dark-colored spots on the general dark-colored background are less noticeable and less contrasting. Pups do not sport a white fur coat as it is shed before or at the moment of birth.

The transverse profile of the tympanic bullae is flattened with an insignificant short step-like drop to the base of the elongated lobe of the external auditory meatus which is almost straight anteriorly and asymmetrically pointed at the tip. The posterior edge of the zygomatic bones has an angular notch; further, the upper portion of the fork has a slightly convex contour (Fig. 91). The rest of the skull features likewise stand in contrast to the corresponding ones of the *larga* (see its characteristics on pp. 323-326).

This subspecies inhabits the southernmost part of the Baltic Sea and from St. Nos in the west to the state boundary in Murman.

Outside the USSR it is encountered throughout the rest of the European section of the range.

3. Island or Kuril seal,⁷⁸ *Ph. (Phoca) v. curilensis* Inukai, 1945⁷⁹ (syns. *chorisii* (?), *stejnegeri*, *nummularis*,⁸⁰ *macrodens*, and *insularis*; the name *richardi* was also used sometimes).

⁷⁸ Known on the Kamchatka and Commander Islands from the end of the nineteenth century under the local name "antrus" or "antur".

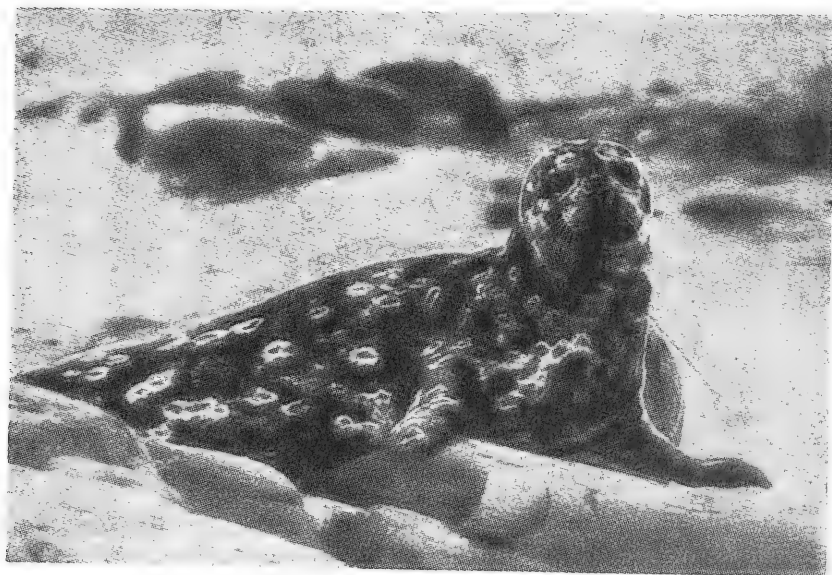
⁷⁹ The first name for this form should be *stejnegeri* J. Allen, 1902 (editor's note). (V.H.)

⁸⁰ See the note on p. 307 (synonyms).

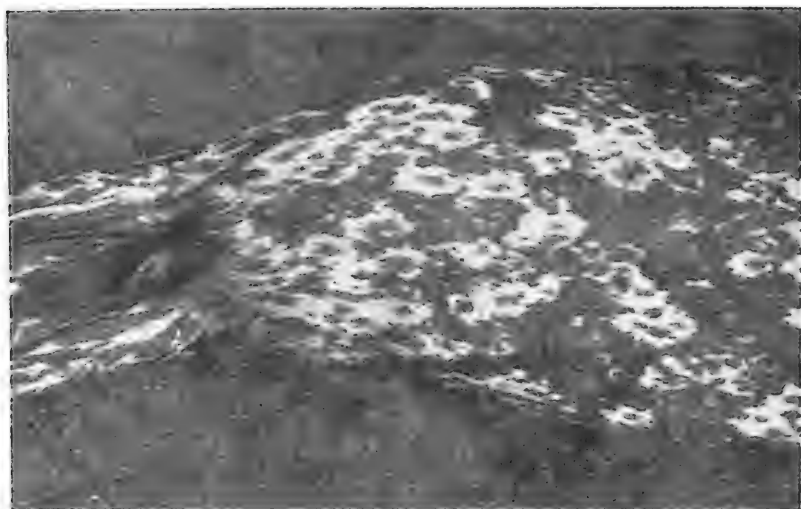
This is the largest form of the species with a body length (along the dorsal curvature) ranging from 140-204 cm; the condylobasal length of the skull varies from 208-247 mm (Belkin, 1964).

Color (Figs. 148-151) varies intensely but an extremely dark, often almost black, main background is a characteristic feature. The ventral side is often very light in color and interrupted by numerous ring-like clear spaces, mostly isolated and dispersed unevenly. Among other animals, the body underside is as dark in color as the upper portion. A broad and obtuse snout is a characteristic feature. Newborns, as in the case of the European common seal, shed the embryonic coat in the mother's womb.

The transverse profile of the tympanic bulla has the same short projection to the base of the lobes of the external auditory meatus as in the common seal, the bony lobe itself being long, set sideways and often pointed. The posterior edge of the zygomatic bones has an angular notch; the longitudinal bony septum in the choanae is usually very poorly developed; a characteristic feature is the angular flexure of the upper contour of the profile in the zone of interorbital constriction. The second and third premolars are usually set obliquely relative to the tooth row. The articular fossae are broadly exposed, flattened. In other skull features,



247 Fig. 148. Dark-colored Far Eastern island seal ("antur"), *Ph. v. kurilensis*. Iturup Island, Kuril, July, 1966 (photograph by S.V. Marakov).



247 Fig. 149. Color details on the ventral side of the female island seal, *Ph. v. kurilensis*, Iturup Island, July, 1966 (photograph by S.V. Marakov).



248 Fig. 150. Variation in dark coloration of the adult island seal, *Ph. v. kurilensis*, Iturup Island, July, 1966 (photograph by S.V. Marakov).



248 Fig. 151. Island seal ("antur"), *Ph. v. kurilensis*, Mednyi Island, July, 1972 (photograph by S.V. Marakov).

there is only a shift in the specific features or they stand between the characteristics of the *larga* and the Atlantic common seal.

This seal is found on the Kuril and Commander Islands and on the eastern coast of Kamchatka.

Outside the USSR it is found on the Aleutian and Pribilof islands and Japan and probably on the coasts of southern Alaska.

The tendency to combine the island seal with the subspecies *Phoca vitulina richardi* found on the American coasts (Moore, 1965*) cannot yet be regarded as substantiated for the simple reason that the skin coloration of these seals differs sharply.

Outside the USSR three more pagophobic subspecies are recognized (Scheffer, 1958; King, 1964): (1) *Ph. v. richardi* Gray, 1864—American waters of the Pacific Ocean from the Alaskan Peninsula to California, and eastern part of the Bering Sea, including the Aleutian and Pribilof
249 islands; (2) *Ph. v. concolor* De Kay, 1842—western Atlantic American

and Greenland waters; and (3) *Ph. v. mellonae* Doult, 1942—Lower and Upper Seal Lake on Ungava Peninsula (eastern Canada).

Craniologically, *Ph. v. richardi* is somewhat closer to the island (Kuril) seal and correspondingly differs sharply from the larga, but the skin coloration of the adults and semiadults of the two is often similar. The range of this seal evidently does not extend in the north beyond Bristol Bay and should thus be limited to the regions free of ice floes (Moore, 1966*; McLaren, 1967*). Insofar as the other two forms are concerned, their morphological features require further study. (K.Ch.)

Biology

Population. It has not yet been possible to determine precisely the population of the common seal (including the larga) in the USSR waters in spite of several efforts in this direction. In some sections of the Sea of Okhotsk a visual count has been made in the rookeries but this has not helped to assess the total reserves of even the larga in the Sea of Okhotsk. Some local populations have been estimated more accurately. Thus in the rookeries on the Kuril Islands the population was put at 5,250, of which 2,000–2,500 constituted island (pagophobic) seals (Belkin, 1964). Very similar figures were recorded even later but without differentiation into island and larga seals: 6,000 on the Kuril Islands, 1,000 on Bering Island, 1,000 on Mednyi Island, and 100 on Seal Island (Marakov, 1970). Insofar as the total population of seals of the subgenus *Phoca* s. str. in the Pacific Ocean is concerned, it has very approximately been estimated in the range of 20,000–50,000 (Scheffer, 1958) to almost 400,000–450,000 (Chapskii, 1966).

Attempts were made toward a more rational census of the seal population. Based on the average area of the ice floes inhabited by lactating animals and their average density (1 to 3 newborn/km², area of "rookery" 150–200 km², and their number in the Sea of Okhotsk and the Bering Sea over 20⁸¹), the maximum number of pups is approximately 15,000. This figure is evidently much less than the actual number.

Different figures were arrived at by the end of the 1960s to the early 1970s. According to aero-visual counts on the spring ice floes, the total larga population in the Sea of Okhotsk was put at 170,000 (Fedoseev, 1971). A similar method had been used sometime before to estimate the larga population in the Sakhalin section of the range. The results were: about 10,000 (with pups) in the region east of the mid-northern section of Sakhalin, about 4,000 in Terpeniya Bay, and 8,000–11,000 in Tatar Strait (Fedoseev, 1970; G.A. Fedoseev).

⁸¹ This calculation was based on the data of Tikhomirov (1966b).

A very large proportion of the total population is concentrated in the Sea of Okhotsk. There is a view that the larga is second to the ringed seal in "natural level of population" (Pikharev, 1940*; Fedoseev, 1966) while its total reserves in this sea are not less than 20-25% of the total population of all species of seals (Tikhomirov, 1966a).

250 The larga is most abundant in the following areas in one season or the other: (1) southwestern Sakhalin part of the sea north of the southern Kuril Islands; (2) western corner of the sea from the Gulf of Sakhalin to Uda Bay, including the Shantarsk archipelago; (3) northeastern part of the sea including Shelikhov Gulf; (4) the region adjoining northwestern Kamchatka; and (5) the coastal belt west of P'yagin Peninsula up to the estuary of the Tauya River. The larga population elsewhere in the continental expanse between Tauisk Bay and the Shantarsk archipelago is evidently much less than in all the regions cited above.

Such a large number of summer-autumn coastal rookeries as found along the coasts of the Sea of Okhotsk is not found anywhere in other parts of the Soviet Far East. The maximum number is concentrated there in the western corner of the sea (mostly in the Shantarsk archipelago and Yamsk-Siglansk region) and along the western coast of Kamchatka. The most detailed information on the distribution and population of the rookeries is available for that part of the sea from the Gulf of Sakhalin to Uda Bay, including Shantarsk Island. The concentrations of the larga here along the mainland beaches are few and rather small, with the exception of Konstantin Bay; at one time there in the 1930s, up to eight rookeries with a total population of 900 to 4,000 seals were reckoned (S. Naumov, 1941; Pikharev, 1941).

The population of the larga is not high in the western part of the Gulf of Sakhalin (S. Naumov, 1941). In Nikolai Bay in 1929, one source put it at 100 or a little more and another source in 1938 at 1,000. The larga is not very rare in Ul'ban and Tugursk bays in autumn. In Uda Bay there are obviously no large congregations. The population is somewhat more on the island rookeries in the Shantarsk archipelago, especially on the Sivuch'i Kamni, Srednii, Ptichii, Utichii, and also Malyi Shantar islands. In 1929, the total population of this region was put at 2,000 (S.P. Naumov, 1941) and in 1938 and 1939, at 16,000 to 18,000 (Pikharev, 1941). The population was the same in 1932 but later doubled (27,500-35,000) (P.G. Nikulin). In some very large rookeries on the Shantarsk Islands, especially on the Sivuch'i Kamni (Shantarsk archipelago), 6,500-7,000 (Pikharev, 1941) or even more (P.G. Nikulin) were reported in the 1930s. In 1958, the total population of the larga in these rookeries was put at 1,000-1,600 (Tikhomirov, 1966).



250 Fig. 152. Larga, *Ph. v. larga* (left) and island seal ("antur"), *Ph. v. kurilensis*, Mednyi Island, June, 1969 (photograph by S.V. Marakov).

251 Considerable concentrations of the larga were noticed in 1929-1930 in the Yamsk-Siglansk region in the fore-estuary expanses at Ireti and Yama and very significant rookeries at Ostrovno, Kamyl, and the Berozovka River estuary. Not even a rough estimate of the population there was ventured. The largas were fewer in Tauisk Bay than in the preceding region; coastal rookeries were few and small in the 1930s (albeit large numbers occurred in the western part of the bay) (Freiman, 1936). In the 1960s, the number of largas in Tauisk Bay was small, barely 2,000. The low population is explained by the relatively high coastal habitation and possibly low food availability (Tikhomirov, 1966).

In terms of larga population, Shelikhov Gulf is next after the Yama region and the western coast of Kamchatka (Fig. 154) but the rookeries there, as already mentioned, are few, especially in the region of Taigonos Peninsula although the data on the former population have been given for only two—Uikan rookery (up to 500) and Cape Verkholsk rookery (up to 400) (Freiman, 1936).

No less than 12,000 seals were counted in the 1930s in 10 rookeries in the Tigil'sk region on the western coast of Kamchatka (from the Moroshchechnaya River to the Tigil' River). The population in some



251 Fig. 153. A herd of largas, *Ph. v. largha*, Karaginsk Island, Bering Sea, July, 1968 (photograph by N.N. Gerasimov).



252 Fig. 154. A section of the rookery of the larga, *Ph. v. largha*, western coast of Kamchatka in the estuary of the Utka River, September, 1967 (photograph by D.I. Chugunkov).

rookeries went up to a few thousand (Tal'nichnoe, 15-20 km south of Cape Babushkina, 3,000-4,000 as also on Cape Utkholoksk) (Lun', 1936). In 1958, six rookeries with a total population of about 6,000 were found in the same region (Tikhomirov, 1966).

The total population of the larga in the western part of the Bering Sea has not yet been determined. It is known that it is not rare along eastern Kamchatka and Koryak Land (from Cape Olyutorsk to Cape

Navarin). It is quite abundant also in the coastal waters of the western and southern regions of the Gulf of Anadyr; by the early 1930s, the proportion of the larga there constituted up to 15% in the local hunters' catch but dropped to a few percent on the Chukchi coasts where this seal inhabits in maximum numbers the Pinkegnei, Tkain, and Privideniya bays (region of rivulets on bald patches) (Freiman, 1935a*).

The population on the Commander Islands, as already noted, is extremely small; it is usually represented by the settled pagophobic form of island (Kuril) seal; the larga is, however, encountered there as a rare find. While only one rookery was known there in the early 1930s with a hundred seals or slightly more (Barabash-Nikiforov, 1936), evidently there are now no less than 15 rookeries (although no exact figure is available). On the Kuril Islands, the island seals have been reported on 28 islands, with pups included on 11 of them (Velizhanin, 1967).

252 During their residence on drifting ice floes, the largas are much more numerous in the central and eastern parts of the sea, especially in the region of St. Matthew Island, in the zone of ice floes south almost up to the Pribilof Islands, and northeast of the latter. Here, in the spring of 1963, over 90% of the seals encountered on ice floes were largas. A nearly similar picture was noticed even in the preceding season; in the more northern regions of the sea, between St. Matthew and St. Lawrence islands, the larga accounted for only a little above 20% (Kosygin, 1966a*; Tikhomirov, 1966). Larga in the Bering Sea has been reported as constituting not less than 30% of the total seal population inhabiting there in the zone of drifting ice floes far from the coasts, and occupies second place after the ribbon seal in terms of population (Tikhomirov, 1966b).

In the other regions of the Far East, considerable concentrations of larga are seen in Tatar Strait although these groups are much smaller than in the Sea of Okhotsk and the Bering Sea. In Tatar Strait the larga predominates markedly over all the other species of seals. The reserves in the Sea of Japan are small; it is evidently maximum on the threshold of Tatar Strait and in Peter the Great Gulf. It has, however, not been possible to express the population numerically.

The population of the common seal in our waters of the Atlantic Basin is extremely small. These seals are particularly rare in the south-eastern Baltic Sea and relatively few on the Murman coasts. It is significant that the coastal people so far have not given their own name to this species.⁸² Only some stray animals were caught in the Murman region after several years, at the very end of the last century (N. Smirnov, 1903).

⁸² At the beginning of this century, this seal was known in Murman as "kamenka".

The seals of this species were not caught in nets, which was the form of hunting in vogue in the 1930s.

- Habitat.* The Atlantic common seal and the Pacific pagophobic forms inhabit selected sections of the coastal zone in a fairly settled manner.
- 253 Within the southern Baltic, on the Polish and German coasts, the seals emerge onto land in the uninhabited sandy or rocky coasts, small islands, spits, and bald patches in the river estuaries and bays. On Murman, they are evidently confined to the bays and estuarine sections of rivers, especially of the Voron'ya; they probably take advantage of the rocky coasts and islets. The Far Eastern pagophobic populations (island seals) select for their rookeries reef ranges and groups of individual rocks, as well as sandy-pebbly coastal sections which offer them protection from the surf (Fig. 155). Such conditions on the Kuril Islands are provided by reefs, small coastal islets, sections of very large uninhabited islands, low rocky ledges, niches between rocks, and coastal shoals (Belkin, 1964a*; Velizhanin, 1967). Some animals (males) at places, for example on the Lovushki Islands, rest on small isolated rocks almost fully submerged in the strait and overgrown with algae (Belkin, 1964b*).



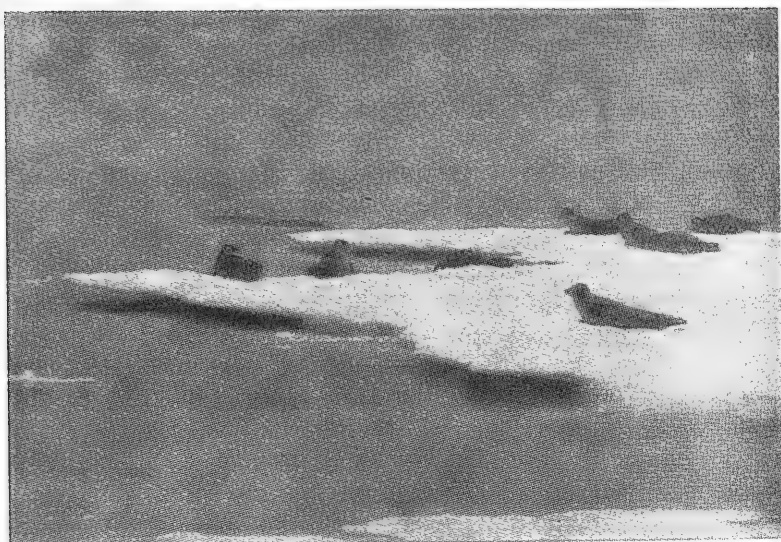
253 Fig. 155. Typical habitat of the island seal ("antur"), *Ph. v. kurilensis*, on Mednyi Island. Commander Islands, Zapalata Bay, June 6, 1962. Sea otters also live here (photograph by S.V. Marakov).

The island seals on the Commander Islands (especially on Mednyi Island) select diverse biotopes for rookeries. These may be sections of the low coast, pebbly or rocky talus zones at the foot of a precipitous cliff, scarps, sloping projections of rocks, etc., especially under reefs protected from the surf. For temporary residence, these seals inhabit large exposed rocky mounds that have been rounded by intense wave action and smoothened by surf abrasion (Marakov, 1968, 1969). The Bering Island population is confined mainly to the region of the Barrier Reef (Marakov, 1967b).

254 The pagophilic seals, i.e., the largas, associated with the coastal land are not permanent settlers since they abandon the beaches jammed by ice floes in winter and spend the winter-spring season on drifting ice floes. There is a distinct difference in the site selection of the larga for whelping, lactation, and molt. Nevertheless, it is important for it that the ice floes be quite stable, clean, without large hummocks, and at the same time not excessively compacted, with an abundance of water pools to provide access to the water. Largas avoid stationary shore ice or a highly compacted mass of broken ice floes. According to some observers, they exhibit a distinct preference for ice floes along the edges (Tikhomirov, 1964) since they are very sparse; according to others, they are encountered not only close to the edge but also far from it, inside drifting ice floes that are highly compacted (Kosygin, 1966). The larga begins to be seen directly on the coasts immediately after the thinning of the ice cover and access to them becomes available. Evidently it appears earliest and in some numbers close to the river estuaries where the ice floes disintegrate usually more rapidly and where the food conditions are more favorable.

Immediately after coming onto the beaches, initially in small numbers and later en masse, the seals begin to move on land to form temporary rookeries. At the beginning of summer, these rookeries appear disorganized and tentative and the animals rest here and there without confinement to any one particular site for long. The islets and spits in the river estuaries that dry up in low tide often serve as rookery sites; where such sites are not available, they are confined right on the gentle beaches in the lower courses of the river itself (Tikhomirov, 1966b). When attracted to the fish migrating for spawning, they themselves enter the estuaries and the lower courses of rivers and even ascend tens of kilometers up the estuary of some rivers.

Transgression into rivers is a regular phenomenon. Evidently there is no single sufficiently deep river abundant in fish in the spawning period which has escaped the notice of the larga. Its long transgressions, sometimes hundreds of kilometers, into rivers such as the Amur and the Anadyr, have long been known. In the former river the larga



254 Fig. 156. Largas on a drifting ice floe in Litka Strait, Karaginsk Island, Bering Sea, early June, 1968 (photograph by D.I. Chugunkov).

was seen even 400 km away from the estuary (Nicol'skii, 1889). In the past the larga ascended 60 km away from the sea along the Sakhalin rivers Poronai and Tyma. Transgressions for 10-15 km were noticed in the Tyma River comparatively recently (Ambroz, 1931). The larga transgresses regularly into many rivers of western Kamchatka such as the
 255 Voyampolka, Khairuzov, Belogolovaya, Tigil', Kavacha, Utkholok, and Sopochnaya, ascending 5-35 km along them (Lun', 1936; Ostroumov, 1966). These seals also enter some rivers on the southwestern coast of Kamchatka.

The larga transgresses for considerable distances into the rivers of eastern Kamchatka. In the 1960s, they were found 35 km from the estuary of the Kamchatka River; a few decades before that they transgressed even farther, up to Klyuchi village and even up to Kozyrevsk, 250 km from the estuary. The larga transgresses for distances of 25-30 km into Zhupanov, Vyvenka, Kultuchnaya, and Apuka. In many other rivers, however, these seals are concentrated close to the estuary, often a whole herd, or transgress only into the lowest courses (Ostroumov, 1966).

Instances of distant transgressions of the common seal, episodic in nature and regarded as exceptional events, have been known in the remote past even in the rivers of Western Europe, especially in the Elba,

in which they were sighted at a distance of 646 km, almost 700 km, and even 757 km from the estuary (Moore, 1955*).

By autumn, sightings in the rivers become increasingly rare and the bulk of the well-fed largas concentrate on the sea coasts close to their favorite haunts, where they form regular (permanent) rookeries.

Groups of isolated rocks smoothened by water and close to the coast or the rocky shore protected from the surf represent preferred sites in the Sea of Okhotsk. In any case there is a distinct preference for land sections submerged in high tide. Sections with an intensely rugged coastline and abounding in reefs and tiny islets meet these conditions to a very large extent. Some dependence could even be established, other conditions remaining comparable, between the degree of ruggedness of the coast and the nature of the rookery: the more rugged the coast, the more rocky it is and the more abundant the reefs on it, the larger the sites suitable for rookeries. Here the seals are more numerous but the number of animals in each rookery is small.

Hunters distinguish three main types of rookeries (Tikhomirov, 1966a). One is the rookery located in a highly rugged locality where sections of large pebbles are interspersed with rocky hummocks and large isolated rocks. Such, for example, are the rookeries on the Sivuch'i Islands. The second type is found on exposed sandy or pebbly laidas (low coastal plains dissected by tortuous rills), islets, spits, gently descending into the water (rookeries on Cape Polonsk, in Tauisk Bay in Melkovodnaya Gulf, and in western Kamchatka in the Moroshchechnaya River). The third, and most common type of rookery, is represented by coastal reefs and rocks, for example on Capes Khairyuzovo, Yuzhnyi, Utkholoksk, etc. (western Kamchatka).

At several places the larga inhabits land together with or in the neighborhood of pagophobic island seals. Such instances are particularly numerous in the northern and southern parts of the Kuril Islands; in the southern parts of the range, largas are even permanent settlers (Belkin, 1964). The biotopes of both forms of seals there are almost identical. A somewhat similar situation is noticed on the Commander Islands where the larga is, however, far less numerous, constituting a rare find in the rookeries of island seals.

Food. The common seal in general is a distinct fish-eating animal but not specialized for a limited number of any particular species and feeds on quite diverse, mainly large fishes available on the coasts at a given time of the year. At the same time, various invertebrates constitute a significant proportion of its food ration.

For nearly two-thirds of the year, from spring to autumn, the larga is assured of abundant fish food. In eastern Sakhalin, in spring, it takes

256 advantage of the approaching herring; in summer it feeds partly on herring and also on humpbacked salmon [pink salmon, *Oncorhynchus gorbuscha*] and Siberian salmon [chum, *O. keta*]. When the summer run (migration) of salmon slackens, the larga takes to consuming river fish—"kundzha," [Sakhalin char, *Salvelinus leucomaenis*] rudd etc. Some seals while chasing these fishes reach far up the rivers. The larga takes to capelin during its en masse availability in the first half of July (Ambroz, 1931).

In western Kamchatka, in late spring and early summer, the larga feeds on char and sea trout which descend from the rivers into the forestuarine regions of the sea, and later on smelt and capelin which form spawning schools on the coasts. Later, from the middle and second half of June, the larga takes to feeding on herring which comes close to the coasts in large numbers. At the end of the herring season, usually from early July, it takes to chasing salmons—chum, red salmon, pink salmon, etc. (Lun', 1936). On the opposite side of the Sea of Okhotsk, on the Shantarsk Islands, it takes to navaga (Pacific navaga [saffron cod, *Eleginus gracilis*]) in spring as supported by the coincident en masse approach of this fish with the increasing population of the seal (Lindberg and Dul'keit, 1929). In Schast'ya Bay (western part of the Sea of Okhotsk) a similar relation has been reported between the gathering of the larga and the availability of smelt in shoals (S. Naumov, 1941). In Tatar Strait, at the end of May, numerous largas were noticed; they were evidently drawn there by the availability of herring.

In the snowy period, when the adult seals are confined to the regions of drifting ice floes far removed from the coasts, the food regime of the seal is somewhat different. Thus in the southern part of the Sea of Okhotsk, not far from the Hokkaido coasts (Wilke, 1954), the larga feeds in April mainly on pollock (*Theragra chalcogramma*) followed by herring, while cephalopod mollusks, especially the octopus (*Octopus daeffeni*), account for a much smaller quantity of food intake. The ratios between these food groups are hardly constant. This seal readily feeds on whatever species are available at the time of foraging for food.

The larga concentrations in the southeastern part of the Sea of Okhotsk, on the Kuril Islands, feed in the spring-summer period quite intensively, consuming roughly equal proportions of fish and cephalopod mollusks. The following fishes were detected in the stomach of largas: Atka mackerel, rockfish (*Sebastes* sp.), walleye pollock, and saffron cod; octopuses from among cephalopods; and squids of the genus *Gonatus* to a much lesser extent (Panina, 1966).

At the end of the reproductive cycle, quite often even after incomplete molting, the larga migrates into the coastal zone, concentrating

mainly in the estuarine sections and the lower courses of rivers where salmon migrate in large numbers for spawning. The seals reach there either at the time of high tide or at a much later period or are even confined to the fore-estuary or bar sections. On the western coast of Kamchatka, in the region of Tigil' River, even brooklets to which the pink salmon go for spawning are quite often literally blocked with the seals, which are caught there in tens or even more. Not being able to penetrate the brooklets, the seals at times even crawl in high tide to the estuary, thereby blocking the entry of fish until their hunger is satiated. Tens of larga transgress into very deep and broad rivers and in rivers such as the Tigil' even 200-300 or more may be seen (Lun', 1936). The same pattern of transgression is seen at other places also. While chasing the fish, the larga can dive under water without respite for up to 400 m, gaining a speed of over 4 m/sec, or it can dart several meters into the air (Chugunkov, 1969).

For 1.5-2 months (August and even September), the seals are not satisfied with the fore-estuary sections but transgress even into the lower courses of salmon-bearing rivers and brooks. This transgression ceases abruptly only in October. Only rare seals, not yet fully fed, hunt for food at this time even in the largest rivers.

The affinity of the larga for coastal sections and rivers abundant in salmon, consuming much and damaging the commercial fish (often snatching only the daintier and meatier portions of the back), is responsible for its reputation as a carnivore inimical to the fishing economy. 257 However, because of incomplete data, it is yet difficult to establish the exact extent of damage inflicted by the larga.

In addition to fish and cephalopod mollusks, crustaceans occupy a definite place in the diet of the larga. Among these crustaceans, the main ones are shrimps and partly amphipods. In Tatar Strait common shrimps of the genus *Sclerocrangon* and amphipods of the genus *Gammarus* have been found time and again in large quantities in the stomach of seals caught at the end of April; in some cases the stomachs were literally crammed with shrimps (Freiman, 1936b). How important shrimps are as food items for the larga in this region is demonstrated by the following data. Of 36 seals caught on May 12-14 in Nevel'sk Bay, the stomach of 21 animals was filled with shrimps; of the remaining 15 caught on May 15-19 in the environs of Cape Lak, the stomach of nine seals also contained only shrimps while the remaining six seals contained shrimps with fish remnants (S. Naumov, 1941).

In the spring-summer period the adult and semiadult Bering largas feed mainly in the morning (up to 9:00 a.m.) and in the evening (after

4:00 p.m.) and consume a large amount of mixed food although fish constitutes the main item at this time. Slightly less than one-half of the seals feed on a single type of food at this time of year: only fish 29%, only crustaceans 11%, and only cephalopods 7% (Gol'tsev, 1969). In Tatar Strait (Gol'tsev, 1971) the larga in spring (in March - April) feeds mainly on pollock, octopuses, navaga, squids, and sand eels. The food of the larga in Peter the Great Gulf has not been adequately studied. Evidently in spring (in March), navaga constitutes the main food followed by flounder (*Liopseta* sp.) and thirdly by perches (of the family Scorpaenidae); in addition to these, the larga there also consumes shrimps (*Pandalus* sp.) (Gol'tsev, 1971).

In the gulfs of Anadyr and Karagin, where studies were carried out for three years (Gol'tsev, 1971), the larga feeds in spring on three groups of animals: (1) different species of fish, mainly the polar cod, pollock, sand eel, goby, and to a lesser extent navaga, armed bullheads (Agonidae), stichaeid blennies, etc.; (2) octopuses; and (3) crustaceans (mainly the shrimp *Pandalus goniurus* and more rarely the following species: *Spirontocaris macarovi*, *Eualus gaimardi*, and *E. fabricii*). Groups of crustaceans, such as amphipods, crabs, and hermit crabs are very rarely found in the stomach (usually in not more than 2%).

The following aspects could be set down with respect to the food of the larga: (1) evidently there are no total or prolonged seasonal abstinences in the feeding of the larga even at the time of molt; (2) the "food spectrum" of the larga is quite broad. Evidently it is this phenomenon that helps them to survive under diverse biotopical conditions which, in the ultimate analysis, explains the unusually extensive distribution of this species, extending from the Chukchi to the Yellow seas; and (3) eurytrophy in turn is ensured by the fact that the large can get at food not only in the shallow and surface sections of the sea, but also at considerable depths, of the order of 300 m or more.

Some other feeding patterns have also been pointed out (Gol'tsev, 1971), especially the daily feeding rhythm: the animals of this species feed mainly in the morning and evening hours. Some age-related changes of food intake were also noticed; the juveniles after lactation feed initially on amphipods, shrimps, and schools of small fishes while the proportion of pelagic fishes (navaga, polar cod, and sand eel) as also cephalopod mollusks increases later. Evidently bits of algae and stones and sand accidentally enter the stomach along with the food and are totally unintentional.

Amphipods disappear from the food of adult largas and the specific proportion of benthic organisms, fishes, and crustaceans (decapods)

correspondingly increases. Among the benthic and demersal fishes consumed are the flounder, halibut, goby, stichaeid blennies, and some poachers; among decapods the snow crab and others. The quantum of cephalopod mollusks consumed also increases considerably.

Although there are no clear ideas so far on the seasonal changes in the feeding intensity of the larga, it is not entirely uniform. During reproduction and lactation feeding is most intense and weakens sharply during molt although food intake does not cease altogether, as shown by the data given above. However, after the end of the snowy period, feeding is again intense. As the seals become well fed, the intake again decreases. In any case, the Okhotsk larga at the end of summer is so well fed that its food hunting impulse weakens sharply. It is at August end and early September that the larga loses interest in food in spite of the continuing arrival of salmon at places and the availability of other food. The larga then prefers to rest on the beach rocks or shoals in the interval between high tides.

Evidently there do exist some minor interruptions in feeding caused by seasonal massive availability of one or the other food items, i.e., short interruptions in their en masse availability, when the numbers of some species decrease and the migration of others has not yet peaked.

The Far Eastern pagophobic (island) seal differs vitally from the larga in its food regime. Being a more settled animal, it relies on various food items available in the region of its habitation which, on the Commander Islands, is restricted to just a mile-long coastal strip (Marakov, 1968). Such a relative stability of habitation of the local populations of island seals is evidently due to the extremely abundant benthic biomass, up to 20-30 kg/m on the coasts of the Commander Islands (Marakov, 1969). Invertebrates play a relatively important role in the food of these Commander Island seals although the seals feed there on fish too, especially the smooth lump sucker *Cyclopterichthys ventricosus*, and, when it is no longer available, on sculpins (genus *Cottus*) and greenlings (Hexagrammidae); from among the invertebrates, they consume predominantly cephalopod mollusks, crabs, even amphipods, gephyreans, etc. (Barabash-Nikiforov, 1936). Instances were also noticed of the intake of rockfish (*Sebastes* sp.) and mysid. In the winter-spring season the Commander Island population survives almost exclusively on invertebrates; these food components, it should be assumed, occupy an important position in different seasons of the year. There are other indications too that smaller fish are consumed by local seals. For example, these seals are not seen in Saranna Bay at the confluence of the Saranna River, which has the most abundant salmon reserves in the Commander Islands, although hundreds of these seals regularly inhabit

the coasts 10 km away from its estuary, on Cape Tonk (Marakov, 1967). Neither were seal concentrations observed around the estuaries of other rivers in spite of the availability of salmon in them.

The corresponding Kuril populations feed on crustaceans (shrimps), cephalopod mollusks (squids) Pacific ruff, bullheads, and other marine animals of the coastal zone (Velizhanin, 1967). Another list of food items has also been given for these same regions: greenling, rockfish, saffron cod (navaga), goby, walleye pollock, flounder, cephalopod mollusks (especially octopuses, more rarely squids) and also diverse types of shrimp (*Crangon dalli*, *Sclerocrangon* sp., and *Lebeus polaris*) (Panina, 1966b).

259 The nearest kin in the American territorial waters of the Bering Sea and in the more southern territorial waters of the USA and Canada, Richard's seal, also feeds on extremely diverse foods. On the Pribilof Islands, as far as can be judged from the limited data (Lukas, 1899*), it feeds in summer mainly on octopuses (*Octopus punctatus*) and to a lesser extent on crabs. On the Aleutian Islands (on Amchitka Island), its food mainly consists of greenling and octopuses (Kenyon, 1965). The more southern seal populations, living beyond the Bering Sea limits, consume mainly fish, including cod, herring, salmon, flounder, rockfish (*Sebastes* sp.), goby, and even skate; they also consume lamprey, cephalopod mollusks, and crustaceans (Scheffer, 1928*; Scheffer and Sperry, 1931; Imler and Sarber, 1947; Fisher, 1952). In the season of spawning migrations of river smelt the seals feed almost exclusively on this fish but, when available, herring becomes their main food item; likewise salmon, when available, is consumed in significant quantities.

Nothing is known about the food of the common seal on the Murman coasts. On the British and Dutch coasts, and generally on the coasts of the North Sea, the food of these seals includes herring, flounder, cod, goby, eel, and occasionally salmon. Shrimps are consumed but less often.

The quantum of the daily food intake, according to the data of zoological gardens, averages 5.5-7.5 kg of fish depending on the age of the animals and the nutritional value of the food; the annual intake thus amounts to 1,800 kg (Moore, 1955*). Taking into consideration the fairly prolonged intervals when there is no feeding in some other seasons, this norm cannot be extrapolated to the food ration under natural conditions. At the same time, the experience of feeding seal pups weighing 17.5 kg at the time of capture on the western coast of Kamchatka, and in captivity at Utkin, confirms the phenomenal appetite of these animals. They do not feed regularly or even daily, but in captivity consumed 1.8-2.6 kg per day of different types of salmon, i.e., roughly 15-19.5% of the pup's own body weight. The young seals voraciously consumed various types

of local salmon: Chinook, masu, pink, chum, silver, arctic, and "Kamchatka steelhead" (with preference for small live fish). On catching a large fish, the larga kills it first by crushing the head between its teeth while small fish are swallowed whole. Larger fish are torn to bits using the teeth aided by the fore flippers. When satiated, the seal desists from fish pursuit (Chugunkov, 1967).

Home range. The distinctly settled population, characteristic of the Commander and Kuril (island) seals, as already mentioned (p. 335), occupies relatively small sections exposed to very little seasonal variation. The Commander Islands are inhabited by individual herds which form extremely close-knit rookeries at various places and remain almost stationary year round. Their precise boundaries have not been determined and establishing them is not easy since the animals in search of food or impelled by other causes can be dispersed quite widely and encountered almost everywhere on the coast (Marakov, 1966*).

The herding tendency of the seals varies sharply in the different seasons while the area covered by their habitation in a given season undergoes wide variation. A herd of 50-100 seals inhabiting an area of a few hundred square meters, entering the water at high tide, is confined within some 3-5 km. But in the winter-spring season the population is "dispersed" in an extensive expanse of drifting ice floes far away from the coasts. This process of animal scattering peaks by spring when the mating pairs are often seen at a distance of several kilometers or many hundreds of meters from each other. The density of largas at the time of whelping in some regions of the Sea of Okhotsk averages 1.2 animals per km² (G.A. Fedoseev). At the end of lactation and mating, they again form groups. Initially these are small and are not as coherent as the much later beach rookeries in which the seals are often disposed shoulder to shoulder. The herd begins to grow only in summer when the animals
260 arrive from every direction and form the final rookeries. The density of such colonies is dependent on the total local population concentration of food items and the nature of the coastline.

Daily activity and behavior. Alternation of periods of wakefulness (activity) and sleep (rest) is mainly guided by the need for feeding and at places, especially in the formation period of the beach rookeries, by tidal conditions. The periodicity of daily activity under the influence of the latter factor is very sharply manifest among the larga of the Sea of Okhotsk in the beach rookeries on islets and reefs that are inundated. Right at the commencement of low tide, the animals gather around an exposed shoal in anticipation of rapid food availability. As soon as the first patch of their favorite land opens up, they rush to occupy the site right at the water's edge. As the water recedes, new animals crawl to

the newly exposed sections of the shoal or reef, forming a large herd in a comparatively short time. Land occupancy and the first residency of animals on exposed land close to one another is accompanied by loud discordant noises, restless movements, and sometimes even scuffles. Ultimately the animals become quiet and begin to rest. They lie somnolently even under unfavorable conditions—frost, rain, or snow—being driven from their place only by a high tide (Lun', 1936).

The animals in the beach rookeries sleep very lightly. There are no special guards in the rookery. From time to time, one or the other seal awakens, raises its head, peers about, and on sighting no danger, drops its head and sleeps again (Tikhomirov, 1966).

A reverse process occurs with the commencement of high tide as the land becomes flooded. The water steadily drives the animals from the peripheral sections and they quietly move sideways in order to gather again at the former site when the tide recedes.

When sleeping or quietly resting seals are disturbed by danger, say the intrusion of man, the entire rookery is instantly enlivened and the animals rush to the water pell-mell like an avalanche. As soon as the danger has passed, they gradually return to their former places on the coast.

Opinions on which of the sense organs are better developed in the larga are somewhat contradictory and the matter still not wholly resolved. According to some, sight and smell (Tikhomirov, 1966) and, according to others, sight and hearing (Marakov, 1966*) are the best developed. Whichever, the larga is one of the most cautious seals.

It is difficult to discuss the daily regime of the larga in winter because of inadequate data. Before the period of reproduction commences, the animals are evidently quite scattered, far away from the coasts among drifting ice floes, and take advantage of open water pools for respiration. The larga usually does not make air holes in the ice. With the onset of the mating period, the activity of the males naturally intensifies. Since ultimately only one male remains for long alongside the female, and the males and females are numerically equal, animal pairing can be assumed as relatively peaceful.

The activity of whelped females is subordinate to the lactation rhythm; in the intervals between suckling her pup the female has sufficient time for rest although she has to ensure the safety of her pup and also feed herself. At the end of the feeding period the adult animals split into groups of some tens each, sleep long periods on a large ice floe or simply rest in a somnolent state. In spring immature animals remain apart from the adults but no information is available on their behavior at this time.

At the conclusion of molt the larga again becomes highly active, partly because of the preceding period of relative abstinence from food. The herds break up and abandon the ice floe. Further, in the period of intensive feeding, the animals attracted by schools of fish again gather into groups. Now, once again, their activity alternates with hours of rest.

The pagophobic (island) seals on the Kuril and Commander Islands are quiet and peace-loving animals with an even more distinct herding tendency than the larga. Their lairs consist mostly of 20-50 animals though some contain even up to a hundred. Quite often the same lair also holds one or more single seals without animosity. Similarly, They exhibit no enmity toward other warm-blooded animals. Scuffles are possible only between the males in the mating season. Affinity for a given site is more pronounced in them than among the larga. While the latter usually inhabit the lower coasts and advance toward the coastline with the receding waterfront during low tide, the island seals can be seen 30-60 m away from the waterline (Velizhanin, 1967). In spite of all their quiescence, however, the screams of the Commander Island seals, similar to those of bitterns, can be heard during the period of lactation; the voice of a female calling her pup in case of danger sounds the same (Marakov, 1966*).

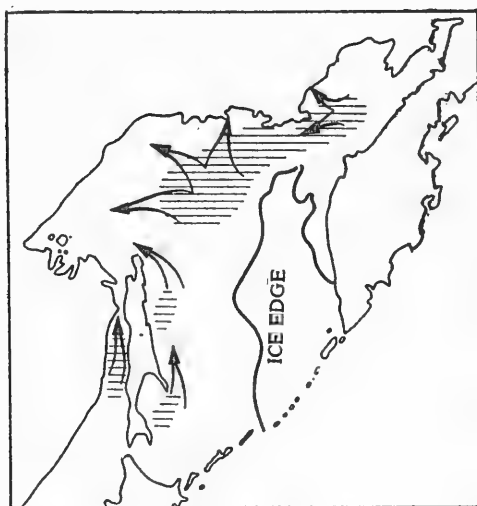
Seasonal migrations and transgressions. These aspects have not been adequately studied. Unlike the harp and some other species of seals, the common seal is usually regarded as a settled animal, albeit this is not entirely correct. Only the Atlantic common seal and the Pacific island seal can be regarded as fairly settled animals. Contrarily, the larga, except for the not so numerous Kuril population, should be regarded as a migratory animal. At least the Okhotsk and Bering populations are such.

Although pagophilic, the larga nevertheless avoids compact ice floes. It therefore abandons coastal regions covered with stable ice floes in winter and returns to them only after the floes break up. The period of its appearance on the coasts depends on the time they are freed of ice floes. In the Sea of Okhotsk, in the Yamsk-Siglansk and Tauisk regions, it approaches the coast for the first time usually at the end of May (Fig. 157). In the Tigil'sk region (Kamchatka) the first, but still very rare, predominantly old, animals are sighted in April. On the contrary, in the Shantar Sea, where the ice floes prevail for a much longer duration, the larga approaches the coast only in July and at some places only in August in some years. Until recently, it was not clear where the largas, especially, the Okhotsk form, spent the winter and early spring months, having abandoned the coast. Some authors assumed that they probably

winter close to the coasts among the drifting ice floes (Freiman, 1936). Others held that some part of the Okhotsk population, perhaps even a significant percentage, winters in the seas of Japan and Kamchatka (S. Naumov, 1941). The second view is supported by the total disappearance of the larga in winter from the Shantar Sea, from Sakhalin Bay, and later even from Tatar Strait.

- 262 Wintering of the larga in the Sea of Okhotsk in the 1950s and 1960s was demonstrated by direct observations. It was assumed that having left the coastal sections for wintering, the larga localized "in certain regions confined to the sites of their coastal rookeries" (Tikhomirov, 1961). Mapping of the main concentrations of the larga showed that by early spring they are at least distributed in "patches" along the periphery of the Sea of Okhotsk, but far away from the coast on the edges of drifting ice floes in the central sections of the basin (Tikhomirov, 1966).

In fact, in the Sea of Okhotsk the seals of most local populations spend the winter-spring period quite far from the land but nevertheless in a "traverse" opposite the coastal sections where the beach rookeries are formed in the middle or end of summer. The animals forced to abandon their coastal sections are attracted toward them in winter and, moving away from the shore ice and in general the stationary coastal ice floes in the zone of drifting ice floes, they continue to remain as long as the ice



- 261 Fig. 157. Figure showing the distribution of the larga in the Sea of Okhotsk during whelping and the main migratory directions to the molting sites in 1969 (by G.A. Fedoseev).

conditions suit them in such places as are closer to the coast abandoned by them. Whether or not the food factor influences the winter migrations of these animals is not known for certain.

Thus the largas scattered in winter and early spring among drifting ice floes in the Kamchatka belt of the Sea of Okhotsk evidently represent the Kamchatka population. The most active among them are sighted in spring along the coasts in the very first favorable conditions. The larga population remaining on the ice in the northeastern fringe of the Sea of Okhotsk is evidently confined to the coastal rookeries of the Yamsk-Tauisk region. The distances separating the closest beach rookeries, according to winter finds of their populations, are at least 150 km in a straight line, which the animals traverse twice a year.

Perhaps even more distant migrations also occur. There is a view that the larga population forming innumerable summer-autumn rookeries on the Shantarsk Islands and around them depart for wintering and for reproduction far southward and winter in the southwestern-most corner of the Sea of Okhotsk, toward the northeastern coast of Hokkaido between La Perouse Strait and the southern part of Sakhalin, on the one hand, and the southern islands of the Kuril range on the other (Tikhomirov, 1961). The autumn-winter courses of the Shantarsk populations to the sites for wintering and reproduction are not known. The spring migrations, however, have been confirmed as running along the eastern coast of Sakhalin (Tikhomirov, 1961, 1966). Thus the large congregations of "whelped larga" noticed in April in the above region in the extreme south of the sea, begin to migrate northward in May along the eastern coast of Sakhalin. In June the largas are concentrated in the region of the northern extremity of Sakhalin and remain there as long as the ice floes prevail. The thawing of ice floes and the disappearance of the seals along with them correspond in time with the arrival of the larga in the Shantarsk region (Tikhomirov, 1961).

Thus, in order to reach its summer-autumn sites, the Shantarsk population (assuming that the pattern of its migrations is accurate) has to traverse a distance of nearly a thousand kilometers. It has to negotiate the same distance back with the approach of winter. The graphic variants of the larga migrations in the Sea of Okhotsk (Fig. 157) agree to some extent with these accounts.

The seasonal migrations of the other populations of the Okhotsk larga are considerably shorter. They are the shortest in the case of some small local groups concentrated in summer on the northern and southern islands of the Kuril range. These groups of larga lead an almost settled way of life, remaining for more than three-fourths of the year near their

beach rookeries. They abandon them only at the time of reproduction, which takes place in the neighboring ice floes (Belkin, 1964).

263 Most of the larga population of the Bering Sea undertake migrations in the same manner as the Okhotsk larga and are dependent on the very same factors—formation of compact stationary ice floes in the winter-spring months on the coasts and migration to the reproduction sites away from the coasts. These sites represent massive drifting ice floes with a fairly large number of open water pools and shore ice, protected simultaneously from storm waves. Most of the Bering population is disposed in the winter-spring months in the eastern part of the sea; the larga from Soviet waters also reaches there.

Seasonal migrations on one scale or another exist among all the populations of the basin of the Sea of Japan. The larga begins to migrate southward from Tatar Strait in November and disappears from there finally in December. It reappears there again in spring only after the thinning of ice floes (Dorofeev, 1936; S. Naumov, 1941). In Peter the Great Gulf the number of larga increases noticeably in autumn and decreases in spring while it abandons these sites almost altogether in summer (Ognev, 1935) and is evidently dispersed widely in the coastal waters to the north and south; some remain in their original sites.

The Far Eastern pagophobic populations of the Kuril and Commander Islands, eastern Kamchatka, and some other sections of the range not exposed to prolonged winter glaciation behave altogether differently. These seals lead a fairly well-settled way of life and undertake no significant migrations whatsoever from their coastal sections. Such behavioral characteristics are evidently typical of the local groups of pagophobic seals inhabiting the Aleutian and Pribilof Islands, coastal sections of Alaska, British Columbia, and the USA. The Atlantic seal belongs to the same type as its migrations occur as a rule within the confines of a limited expanse inhabited by various populations. These seals migrate under the influence of weather and human persecution, food availability, need for more isolated sites for reproduction, and other factors, as exemplified by the behavior of the Dutch populations (Bemmel, 1956).

Reproduction. The pagophilic (larga) and the pagophobic (island) seals mate at different times. Among the former, this period sets in earlier. In the Sea of Okhotsk and the Bering Sea the larga mates soon after whelping. The presence of an adult male hanging around almost each suckling female is the first sign of mating activity. These observations have been supplemented by a study of the genital organs (including the presence of sperm in the vagina). The total period of mating

in the northern part of the Sea of Okhotsk and in the Bering Sea continues for about one month, from April 20 to mid-May; the bulk of the females, however, mate in the period from May 1 to 10. Mating pairs start to form roughly one week or 10 days before whelping and break up by the commencement of the period of molt (Tikhomirov, 1964, 1966).⁸³

In the more southern regions of the Soviet Far East, in the southern parts of the Sea of Okhotsk, and in the Sea of Japan, mating occurs early, corresponding to the much earlier periods of whelping, i.e., in March and April (Tikhomirov, 1966a).

264 The island seals reproducing on the coasts, in the Kuril and Commander Islands and on the coasts of eastern Kamchatka, have not been adequately studied in this regard. Mating of the Commander Island populations occurs at the end of May (Barabash-Nikiforov, 1936) or more probably in June-July (Marakov, 1964*, 1966*); it occurs obviously at May end and in June on the Kuril Islands (Inukai, 1942; Belkin, 1964). Information about the mating season of the seals on the Murman coasts is not available. It is also not available for the population entering the Soviet Baltic waters. In general, however, the European, especially the Scandinavian, populations of the common seal have long been thought to mate in the autumn months: in September (Holmgren, 1865; Lilljeborg, 1874) or even early October (Collett, 1911 - 1912). The mating of seals on the southern coasts of the North Sea has been placed in August (Havinga, 1933; Moore, 1952*, 1955*). Despite the earlier views followed by several Soviet authors (Ognev, 1935; Bobrinskii, 1944*; Vinogradov, 1949; and others), the European common seals mate at the end of July and in August (Harrison, 1960). Among the American (eastern Canadian) populations of the Atlantic common seal, mating occurs not in the autumn, as was thought earlier, but immediately after lactation ceases, i.e., June end or early July (Fisher, 1954).

As in the case of other seals, there is no distinct polygamy among common seals albeit the bulls in one way or another claim the right to mate with a particular female. Furious and prolonged scuffles evidently do not occur among them although marks of seizure in the form of

⁸³ In the light of these data it is difficult to agree with the earlier viewpoint (Sleptsov, 1943) that the Okhotsk largas mate late, from June through the first half of August (peak at July end), when most of these seals have already completed molt. S.P. Naumov (1941) places the mating of the Okhotsk larga as late as August-September, restricting it thus to the coastal rookeries in which it is assumed to occur.

E.S. Chuzhakina (1955), using this very information, contradicts herself a few lines later by correctly pointing out that mating precedes molt, which occurs from April end to early June.

scratches and scars are often seen on the skin of the Atlantic as well as the Pacific pagophobic seals (Allen, 1880; Havinga, 1933; Averin, 1948). Among the larga, fights for the possession of a female are evidently few. The literature adduces neither direct evidence on scuffles among males, nor indirect evidence. The skin of the males reveals no injuries inflicted by competing suitors. In general, the period preceding the formation of mating pairs, noticed from the commencement of lactation, proceeds imperceptibly among largas.

Direct observations of the act of mating of the larga have also not been reported in the literature. On the coasts of eastern Kamchatka, it was observed in water on July 7, 1942 (Averin, 1948). The region, as also the date of observations, indicate that the mating seals in this case were probably pagophobic island seals. On the coasts of Scotland, eastern England, and Holland, mating of the common seal was invariably observed in water (Havinga, 1933; Venables and Venables, 1957; Harrison, 1960).

Mating pairs of island seals (the male pursuing the female in water) can be seen on the Commander Island coasts in calm weather in June and July. Both animals loudly whip the water incessantly with the hind flippers, often dive, and on surfacing sniff each other's snout (Marakov, 1966*).

A study of the genitals and vaginal smears convincingly demonstrated that ovulation of the Bering larga commences even around the 20th of April, with peak mating in the first 10 days of May (at this time, only virgin females and those that have not whelped in the current year mate), while the total duration of the mating season extends from April 20 through May 15; by this last date almost all the females are inseminated (Tikhomirov, 1964, 1966, 1970). These periods apply to a great extent to the Okhotsk larga also.

No unanimous opinion was available until recently about the duration of gestation. The assumption of late (autumn) mating and differences of opinion regarding the existence and duration of a latent period gave rise to controversies in determining the duration of gestation also. It was assumed as seven months (S. Naumov, 1941), nine months (Sleptsov, 1943; Chuzhakina, 1955; Venables and Venables, 1955), close to ten months (Havinga, 1933; Scheffer and Smith, 1944*), or 11 months (Moore, 1952*, and others). At present, a fairly long (two to four months) lag in the implantation of the blastocyst is recognized among the pagophobic seals (*Ph. v. richardi*) and largas (Fisher, 1954; Harrison, 1960).

265 Thus, of the nearly 10.5 to 11 months, on average, from the time the female mates up to her parturition, active embryogeny lasts only seven to nine months.

Twins have not been reported among largas while they are not altogether rare among the European common seals. Thus, of the 12 births recorded from 1933 through 1940 in the Bremerhaufen zoological garden, two were twins (Moore, 1955*). Of the 70-80 births occurring annually in nature in these same years on the coasts between Vezer and the Elba, about 10 were twins (Juncker, 1940). In the Far East the larga becomes capable of reproduction at three years of age at the earliest but the majority about one year later. Some animals even after attaining maturity lag behind until the fifth and even the sixth year of age (Fedoseev and Shustov, 1964*; Tikhomirov, 1966). Immature females at four years of age constitute 7% and at five years 6%. All males are mature from the fourth year of age (Tikhomirov, 1968). The island seals have not been adequately studied in this respect; it has been assumed that maturation of the Commander seals sets in at the age of two to three years (Marakov, 1966*). The European common seals are capable of reproducing in the third or fourth year of age (Havinga, 1933; Heinroth, 1958).

By the time maturity is achieved, the testes of the larga weigh at least 100 g (without appendages), rising to 185 g by the mating season (Tikhomirov, 1966d*).

No data are available on the time of whelping of the common seal inhabiting the Murman coasts. In the Norwegian waters, however (in the southern as well as northern parts), the seals whelp roughly at nearly the same time, from the first half of June to July 20, predominantly at the end of June (Collett, 1911-1912; Eines, 1964*). Along the southern and western extremities of the North Sea and in the southwestern Baltic Sea, pups begin to be seen in most cases in the second half of June to mid-July though much earlier as well as much later dates of birth are known (Havinga, 1933; Wagner, 1936; Venables and Venables, 1957; Harrison, 1960; Moore, 1955*, 1965*; and others).

In the Pacific Ocean part of the range, the pagophobic (island) seals of the more southern populations forming rookeries on the Kuril Islands whelp from mid-May through the second half of July (Belkin, 1964, 1966; Velizhanin, 1967); those on the Commander Islands mainly do so in June (Marakov, 1964). The much earlier dates pointed out for the latter region, i.e., from April end through early May (Barabash-Nikiforov, 1936), are evidently not wholly accurate or pertain to the pagophilic larga.

Largas whelp in a much earlier winter-spring season. Those on the southern boundaries of the range in Peter the Great Gulf whelp right in February (Ognev, 1935; Nikulin, 1937) and even at the end of January (Pikharev, 1948). According to the latest data (Kosygin and Tikhomirov,

1969), the period of whelping in this region extends "roughly from the middle 10 days of February and includes the first 10 days of March". In Tatar Strait this period shifts to a much later period. A large number of females give birth there in March and the remainder in April; the total period of whelping, however, extends from mid-February to the second half of April. Instances are known of pups being caught there even on May 19 (Dorofeev, 1936; Nikulin, 1937; S. Naumov, 1941; Pikharev, 1948; Tikhomirov, 1966; O.A. Salmin).

In the Sea of Okhotsk, the pups appear earlier in the south, mainly in mid-March, than in the north where whelping in most cases occurs in mid-April (Tikhomirov, 1966). In general, however, this period even in the southern part of the sea is also evidently extended since, in the region of the southern Kuril Islands, newborns were sighted on the ice floes at March end to the first half of April (Belkin, 1964).

266 Newborns were noticed at the earliest in the Bering Sea in 1962 on April 3 (Tikhomirov, 1964) and in 1963 on March 26 (Kosygin, 1966). Until the beginning of the middle 10 days of April, however, pups were very rare and most of the adult females caught at this time were gestating. En masse whelping occurs there from the second week of April and extends roughly to the end of that month, peaking in the middle of the month. Newborns were seen in 1963 up to mid-May (Kosygin, 1966). The solicitude of the mother for her pup in the period of lactation is great; she does not tolerate even the proximity of people or ships, considering them a mortal threat to her offspring.

The larga usually whelps every year; in any case, barren females hardly exceed 10%.⁸⁴ In the period of reproduction the maternal population and the bulls are concentrated mainly in the pelagic strip of drifting ice floes 20 km or less wide (Tikhomirov, 1966b) though in the Bering Sea they whelp even deep among sparse ice masses (Kosygin, 1966a). The larga selects for whelping ice floes that are not particularly large and preferably not too hummocky but firm and clean with open water pools among them. They do not whelp on compact stationary ice floes (in the coastal fast ice) and within intensively broken massive ice. Parturition occurs not far from the edge of the ice floe.

These seals do not form concentrated nurseries and whelp far from each other; but in Tatar Strait scattered groups of females, sometimes with up to 20 to 30 pups in the range of vision, have been observed. In the Sea of Okhotsk and in the Bering Sea they remain more scattered,

⁸⁴ According to E.A. Tikhomirov (1966), it is roughly 5% of the eligible females; Gol'tsev and Fedoseev (1970) assume it to be 15% for the Okhotsk population and 8% for the Bering population.

usually at a distance of at least 0.5 km from each other but sometimes even farther apart. Thus no more than two or three suckling females with pups are seen in 1 km² (usually with an adult male alongside). On the whole, the area of the ice floes thinly populated with animals extends for 150-200 km² (Tikhomirov, 1965b*). Even the term "rookery" cannot be applied to such thinly scattered seals.

The pagophobic Commander Island seals undergo parturition sometimes on the coastal rocks or in sand spits which are sometimes even flooded during high tide so that the pups in such cases are "introduced" to the water immediately after birth (Marakov, 1967). The newborn is quite prepared for this: it is born with a short hair coat, having shed the preceding embryonic fur in the mother's womb. The island seals, also on the Kuril range and outside the USSR waters on the Aleutian and other islands, undergo parturition under fairly similar conditions. The seals inhabiting the more southern regions of the Pacific Ocean coasts of North America whelp on sandy-pebbly shoals (especially in the estuarine sections and the lower courses of rivers) and also on small rocky islets and reefs along the continental coast. The Atlantic seals along the coasts of the North Sea, in the southwestern Baltic, and in all the other parts of the range, including Soviet western Murman, undergo parturition under nearly similar conditions.

Growth, development, and molt. Newborn largas weigh 7.5-8 kg, somewhat more, possibly up to 10 kg in some cases. The body length in a straight line (*Lcv*) varies from 65 to 80 cm (length measured up to tip of tail along the body curvature varies from 75 to 90 cm and pups already somewhat grown up to 110 cm). They have the typical white coat of dense, long, silky hairs of almost pure white color with creamy tones and resemble the white pups of other pagophilic seals, especially of the harp and ribbon seals.⁸⁵ Their teeth still sit deep in the alveoli and are covered by the gums. Their milk teeth, however, are extremely reduced and may be imperceptible. The subcutaneous adipose tissue has almost not yet developed.

267 The pups of the Atlantic common seal born on the beach almost do not differ in size and weight from the pups of the larga,⁸⁶ are devoid of the embryonic coat, and are born almost covered with the short, smooth, coarse hair coat that is characteristic of older animals. However, during

⁸⁵ The hair coat of the newborn in the region of Peter the Great Gulf is a smoky-gray (Kosygin and Tikhomirov, 1969).

⁸⁶ The maximum of 15 kg (Havinga, 1933) should be regarded as an exaggeration; evidently this pup had already completed suckling.

the embryonic growth of this seal and other ecologically similar pagophobic seals, i.e., Kuril (island) and Richard's seals, the embryonic white coat is seen, as in the larga. Just before birth, the hair coat loses strength and most often is shed immediately before parturition or right at the moment of birth, more rarely in the first few hours after birth. Only in extremely rare cases do the pups sport this coat for a few days after birth. Yet many such extraordinary cases have been recorded in the last 20 years (Moore, 1965*; Stutz, 1966).

Since the newborn pagophobic seals have no embryonic coat, they can enter water within a few hours of birth. As noted above, such pups may even be born right in water; in such cases the pup nevertheless scurries toward land with the mother's help. The pup of the common seal has a color similar to that of the adult but with a more distinct monochromatic middorsal strip.

Suckling of larga pups continues (as far as can be judged from the average birth periods and from the time at which the female abandons her pup) for about one month. For much of this time the mother remains on the ice floe, never leaving her pup and displaying extraordinary solicitude. In the Bering Sea lactation continues from April 10 to May 10-15 (Tikhomirov, 1964). In this interval the pup adds 12-20 cm and measures 80-90 cm in a straight line or 95-107 cm along the body curvature (Kosygin, 1966) or 101.5-111 cm (Chapskii, 1967). The pup grows rapidly during lactation and its weight increases largely as a result of fat deposition. At the end of suckling the initial weight of the newborn quadruples to 30 kg or more.

As this period draws to a close, the embryonic coat weakens, is later gradually shed, and soon replaced by a new smooth, short, and very firm coat with sparse hair. Opinion on the duration of the primary embryonic coat is not unanimous. According to some, it remains strong for roughly two weeks or slightly less (Tikhomirov, 1964) and in the Bering Sea up to April 15; according to others (Kosygin, 1966), only 5-7 days, the pups being fully molted at 15 days of age (Fig. 158). Casting of the embryonic coat proceeds in the very same sequence as in pups of other species of seals; after a brief latent period during which the embryonic coat loses strength and the new coat still covered with short and smooth hairs grows, molting commences and the old embryonic fur is shed in clumps on large sections of the head, flippers, and tail. In this state, given the sharp contrast between the dark-colored molted sites and the still preserved light-colored embryonic fur, the pups appear to sport a white fur vest (Kosygin, 1966). Later, the hairs on the back and on the ventral side of the trunk are shed. Most pups of the larga are completely free of their embryonic fur by mid-May (Tikhomirov, 1964).



268 Fig. 158. Intensely molting white large pup. Bering Sea (photograph by G.M. Kosygin).

268 Only on completion of molt does the pup begin to enter water and adjust to the new environment, remaining in it almost up to autumn. The color of the new hair coat after the embryonic coat has been shed is very similar to that of the adult but is also variable with near total absence of light-colored streaks along the spine.

The total duration of lactation of the Kuril (island) seal is considerably more extended: 3.5 months from mid-May through August end (Velizhanin, 1967). This is evidently due to the prolonged whelping season. The individual duration of suckling, though undoubtedly short, is evidently much longer than the corresponding duration in the larga. Many newborns of the island seal originally sport a very deep dark, almost black, coat with diffuse light-colored annular spots. Their body length along the dorsal curvature (L_c) varies from 94 - 104.5 cm and they weigh 19 - 19.4 kg (Belkin, 1964). There is no information on the increase in these values after lactation.

The duration of lactation among the European common seal (British population on the east coast) is thought to be three weeks (Harrison, 1960). For seals on the coasts of Holland, the Federal Republic of Germany, and the German Democratic Republic, double this duration has

been indicated. There is basis for preferring the data of direct observations on the duration of suckling of the animals born in zoological gardens, which indicate a figure of six weeks (Heinroth, 1958).

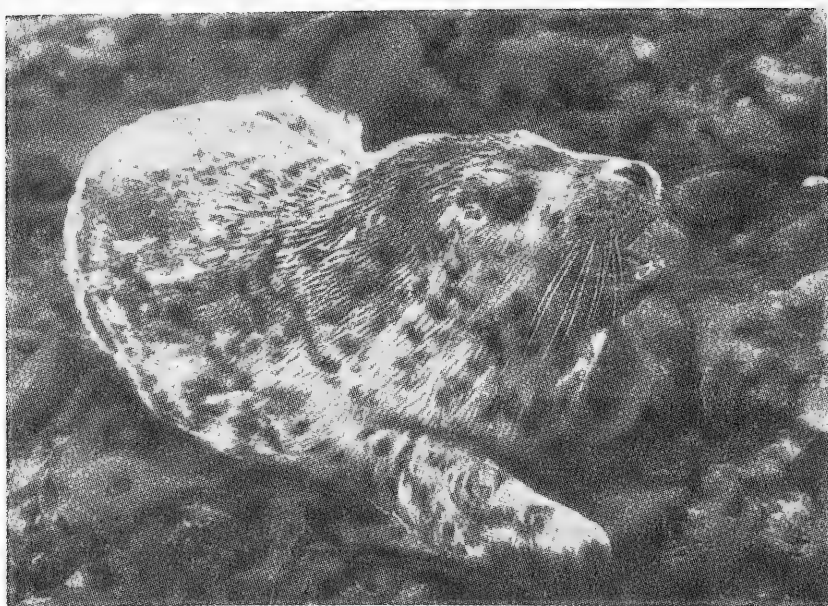
The rapid growth and weight increase of pups of all seals, including those of the species under consideration, over a comparatively short duration of lactation is explained by the very high nutritional value of the milk. The milk of the common seal has 45% fat and 9% protein (Harrison, 1960). Later, the growth and development of the youngster feeding on its own are characterized by slow tempos. It has been indicated (Havinga, 1933) that, after the first year, the Dutch seals grow to 95.7-113 cm (length in a straight line, *Lcv*); this is only 5-10 cm more than the length achieved by the pup of the larga in less than a month of lactation. Further growth of the larga is illustrated in Table 14 (Tikhomirov, 1968).

The molting of immature (commencing from yearlings, Fig. 159) and adult largas is mainly confined to the regions of reproduction and only partly to the beach rookeries where probably some adult animals may complete molt, if they have not completed it on the ice floes. In the Sea of Japan, only one molting region is known for certain in the northern part of Tatar Strait. The molting sites of the larga reproducing in Peter the Great Gulf are not yet completely known. It may be assumed that the animals spend a part of their molting period there itself on the ice floes and complete the molting process on the coastal reefs.

In the Sea of Okhotsk molting colonies have been detected in the southwestern region of Shelikhov Gulf (in Yamsk Bay), in the northern part of the Sea of Okhotsk itself, west of Shelikhov Gulf to Tauisk Bay, and on the eastern coast of Sakhalin. The local groups perhaps molt also in the proximity of the western coast of Kamchatka. Opinions vary concerning the westernmost part of the sea, i.e., Gulf of Sakhalin and the Shantarsk archipelago. According to some (S. Naumov, 1941), there are no genuine molting colonies of the larga in the Gulf of Sakhalin;

Table 14. Body length of the larga along the dorsal curvature (*Lc*), (cm)

Age in years	Female		Male	
	Range	Average	Range	Average
1	105-136	123	113-136	125
2	120-143	134	132-150	140
3	137-150	143	142-160	151
4	141-155	149	159-161	160
5	140-152	149	148-165	162



270 Fig. 159. Under-yearling larga. Bering Island, May, 1969 (photograph by I.P. Tomatov).

at the very end of the icy season “only insignificant remnants of molted colonies formed in the other regions” are seen there. In fact, throughout June the larga is mainly confined to northern Sakhalin, or even farther away, toward the Gulf of Sakhalin and more so toward—Shantar Sea [Island], which is blocked by heavy ice floes. Only in the second half of this month does the larga localize in a comparatively restricted space between Cape Litke and Men’shikov Island. This region represents the main residence of the larga in spring, on drifting ice floes all along the western part of the Sea of Okhotsk. The seal penetrates west of this region only from the first half of July, by which time most of the animals have completed molting (Pikharev, 1941). Other authors unreservedly include, in addition to the above regions, not only Sakhalin Bay, but also the Shantar Sea [Islands] among the molting regions of the Okhotsk larga (Nikulin, 1937; Tikhomirov, 1966).

In the Bering Sea the main concentrations of molting largas are seen in the same two main regions in which whelping occurs: the southeastern fringe of the ice masses (mainly to the north and northeast of the Pribilof Islands), the Gulf of Anadyr and partly the eastern coast of Kamchatka. Molting largas do not congregate in the Chukchi Sea (Tikhomirov, 1966); there are no accurate data whatsoever on the molting of this seal there.

The information available in the literature on the period of molting varies widely. In Tatar Strait molting occurs at April end and in May (Dorofeev, 1936) or at the end of May (Yu.A. Salmin). In the Sea of Okhotsk, on the eastern coast of Sakhalin, molting larga juveniles were encountered (in twos and threes) on small broken ice floes at the end of May (Nikulin, 1937) and somewhat farther away from Sakhalin but in the same southwestern part of the sea molting adults were encountered at the beginning, middle, and end of June (Pikharev, 1941); further, in 1939, an adult larga caught on June 17 was still in the initial stage of
 270 molt while others caught later (up to July 1) were at the peak of molt. In the northern part of the Sea of Okhotsk the first of the molting largas were found among the molting bearded and ringed seals from May 20 (Freiman, 1936). On the whole, the molting period in the Sea of Okhotsk continues, according to some (Tikhomirov, 1961), from the end of April and, according to others (Fedoseev and Shustov, 1964), from around May 10 to mid-July, i.e., roughly over a period of 2-2.5 months.

In the Bering Sea most of the adult largas generally molt during the same period: from the middle or end of the second ten-day period of May to the middle or even the end of June. It has been pointed out that males and females (which for some reason have not undergone parturition) begin to molt 10 to 15 days earlier (it is quite possible that some males molt even during the mating season) compared to females that have whelped (Tikhomirov, 1964). Young animals, however, molt somewhat earlier than the adults, from the last 10 days of April (Kosygin, 1966), although the reference to a much earlier period, i.e., from the first few days of March (Tikhomirov, 1964), is due to an incorrect understanding (or pertains to the southernmost populations). More recent authors (Gol'tsev and Fedoseev, 1970) have indicated that en masse molting of the larga occurs in June.

Information on the molting of land-loving forms is extremely scant. Only general references are available on the European-Atlantic seals which undergo molt in summer (Millais, 1904; Collett, 1911-1912); young seals molt earlier, in July, and older ones in August and even early September (Havinga, 1933). The first signs of molting among the pagophobic island seals inhabiting the Kuril Islands are noticed early in July. At the end of this month and in early August, intensely molting animals were noticed on Makaarushi Island; molted animals were caught in mid-August (Belkin, 1964).

On the Pacific coast of Canada and the USA (especially on the coasts of British Columbia and Washington state), molting continues from the first half of August to September end (Fisher, 1952).

- 271 *Enemies, diseases, parasites, mortality, competitors, and population dynamics.* The common seal in the Baltic section of the range is threatened by no natural enemies. One of the most important factors responsible for natural mortality there is stormy weather, which can take a toll of newborns. Some pups may perish due to unfavorable birth conditions, as sometimes happens in zoological gardens. Nothing is known about the natural mortality of the Murman populations of the common seal.

Information on the larga in this respect is more specific. Although itself quite aggressive, it is attacked at places by carnivores. Bears attack the larga in many regions on the coasts of the Sea of Okhotsk during the formation of beach rookeries. Sometimes bears even stack their quarry in some ravine and cover it with soil. Largas torn apart by bears have been found time and again along the banks of the Moroshchechnaya River in western Kamchatka and in some bear dens along the northern coast of the Sea of Okhotsk, including Amakhton Bay (S. Naumov, 1933, 1941; Tikhomirov, 1966). There is evidence of wolves attacking the larga. A body with the internal organs and brain eaten out was found on the same Moroshchechnaya River with many wolf tracks around it (Tikhomirov, 1966).

Even large predaceous birds can peck a newborn larga to death. An indirect proof of this is the hovering of the golden eagle and the bald eagle around seal rookeries. The Kamchatka residents on the coasts of the Sea of Okhotsk speak of seal fights with eagles. On the ice floes close to Sakhalin, pups of the larga pecked to death by eagles were also seen (Inukai, 1942; Wilke, 1954). A similar instance was noticed in the Bering Sea too on the coast of Alaska (Wilke, 1954). Nevertheless, instances of predaceous birds attacking pups, less so fully grown largas, are not very frequent since the breeding sites of the latter are usually quite far from the coasts; further, the adult animals protect their offspring.

The shark could be regarded as a natural enemy of the larga though no concrete data are available for recent years. This factor has been cited for the Atlantic common seal (Sutton and Hamilton, 1932*). At places, the larga is victimized by the killer whale (*Orcinus orca*). On the Japanese coastal whaling base near Abashiri, seals of this species were the most frequent food item found in the stomach of killer whales caught from August through October, 1948 (Wilke, 1954).

Abiotic factors are equally responsible for the mortality of the young. Pups on sparse drifting ice floes among extensive open water pools and more so on being transported to the fringe are exposed to dual fatal factors. In highly windy weather the embryonic fur coat sprayed or even drenched by an icy wave simply cannot protect the pup from cold. A powerful wave can sweep a pup off an ice floe or even topple a floe with

pups into the water. Ice floes quickly break up under wave action and are transported to more southern regions where they soon disintegrate and thaw. Contrarily, during hummocking of ice floes, pups face the danger of being crushed. Every year, from April end to the first 10 days of May, carcasses of larga pups in white fur coat are scattered on the coast of eastern Kamchatka. Particularly large numbers of them were thrown up from May 1 through 5, 1942. On the coast of Kronotsk sanctuary, in Ol'ga Bay, 17 such dead pups were collected (Averin, 1948). These have been regarded as important food supplements to bears awakening from winter slumber.

Insofar as the Pacific pagophobic island seals are concerned, especially those inhabiting the Commander Islands, they have practically no natural enemies except the blue fox, which attacks newborns only as a very rare exception (Marakov, 1966*). There are apparently more enemies on the Kuril Islands but practically speaking, neither the bear nor
 272 the wild dog, nor even the fox can inflict harm since the rookeries are generally located on small islands or on reefs where the seals are inaccessible to the carnivores.

Our literature contains no definite data on the diseases of this seal. Among the external parasites recorded, the louse *Echinophthirius horridus* localizes mainly on the back, upper side of the tail, and at the base of the hind flippers, often in large numbers (Freund, 1933; Moore, 1955*). This parasite is a carrier of microfilaria in the blood.

Information on the helminth fauna of the Atlantic common seal appeared for the first time in the early nineteenth century (Rudolphi, 1819). Later, the helminth fauna of this seal was studied quite thoroughly (Monticelli, 1889; Reie, 1899*; Stiles and Hassall, 1899; Linstow, 1905; Ransom, 1920; Baylis and Daubney, 1925; Lyubimov, 1927; Delyamure, 1955; and others) but the helminth fauna of the Far Eastern larga had almost not been studied until quite recently. Only nine species of helminths of this seal were known by the early 1960s (Belopol'skaya, 1960). Much progress has been made in recent years in identifying the helminth fauna of the larga. In 1966-1967, 152 animals were autopsied for helminthological studies: 116 from the Bering Sea and 36 from the Sea of Okhotsk. As of date (M.V. Yurakhno), 29 species of helminths and 4 of their larval forms have been identified in the Atlantic common seal and larga. From among the trematodes these were found: *Orthoplanchnus arcticus* (infects the liver, gall bladder, and pancreas; from 1 up to 69 specimens were detected in a single animal), *Cryptocotyle lingua*, *Echinostoma acanthoides*, *Rossicotrema venustus*, and *Phocitrema fusiforme* (parasites of the intestine), and *Pseudamphistomum truncatum*

(liver). From among the cestodes these were found: *Diphyllbothrium cordatum*, *D. hianus*, *D. schistochilus*, *D. latum*, *Diphyllbothrium* sp., *Pyramicocephalus phocarum*, *Diplogonoporus tetrapterus*, *D. mutabilis*, *Trigonocotyle skrjabini*, and *Trigonocotyle* sp. (all these species of cestodes infect the intestine). The nematodes infecting the gastrointestinal tract are: *Anisakis* sp., *Contracaecum osculatum*, *Phocascaris phocae*, *Terranova decipiens*, *T. azarasi*, *Terranova* sp., and species of genera of Anisakidae; *Skrjabinaria spirocauda* infects the heart, blood vessels, and lungs; *Parafilaroides gymnurus*, *P. krascheninnikovi*, and *Otostrongylus circumlitus* infect only the lungs; the nematode *Ph. phocae* infects the large more often than other seals. The acanthocephalans infecting the intestine are: *Corynosoma strumosum*, *C. semerme*, *C. validum*, *C. hadveni*, *C. ventronudum*, and *C. osmeri*.

The helminth fauna of the Atlantic common seal and the large vary significantly. There are large differences in the species composition of trematodes and cestodes; there is none common among the 14 species and, further, these groups of helminths are more abundantly represented in the large. The latter is highly afflicted by helminths, especially in the Bering Sea, where all the animals commencing from yearlings were found infected by hundreds and even thousands of *C. strumosum* (there were more than 10,000 of them in some individuals) and also by a large number of other helminths, among which the cestode *T. skrjabini* was the most numerous (from a few tens to some hundreds) (M.V. Yurakhno). The more commonly infected organs were: small and large intestine (80% of the animals), stomach (72.2%), duodenum (66.9%), and rectum (60%). The following organs were more rarely infected: liver and gall bladder (7.8%), lungs (6.9%), heart and large blood vessels (5.3%), and pancreas (0.9%). The most pathogenic helminths of the common seal include *S. spirocauda*, parasitizing the heart, large blood vessels, and lungs.⁸⁷

- 273 The population dynamics of seals in our territorial waters and in the seas of the Far East has practically not been studied in recent decades. The degradation (which was not very intense) of some beach rookeries of the large in the 1930s in the region of Tatar Strait and at some points on the coasts of the Sea of Okhotsk as a result of hunting was minimal and intermittent and hence led to no particularly serious consequences (see pp. 364-366). Hunting from ships in recent years in the Sea of Okhotsk

⁸⁷ Information on the helminths of the species under study published here was specially prepared for this publication by Prof. S.L. Delyamure and A.S. Skryabin, scientists at the Helminthological Laboratory, Crimean State University.

and the Bering Sea (see p. 365) has likewise exerted no perceptible influence on the population of the larga. Only some local populations of pagophobic seals, especially on the Commander Islands, have not so far regained their earlier population level due to uncontrolled hunting. The Kuril seal too possibly shares the same fate. The extremely small population of Baltic seals is explained as a result of hunting and the high degree of economic exploitation of the coasts, particularly the marginal sections of the range. The small Murman populations at present have clearly gained the maximum levels.

While calculating the reproductive capacities of larga populations, the following basic data should be taken into consideration: (1) the quantitative proportion of the males and females remaining equal, the mature animals in the populations of the Sea of Okhotsk and the Bering Sea average 55.7%; (2) barrenness among the females is not identical in both populations but is generally not high (8% in the Bering Sea and 15% in the Sea of Okhotsk populations). Thus the annual increment is about 25% of the total population; (3) the mortality of underyearlings is high at an average of 42.5% pups and thus the increment in herd is roughly 14.5%; and (4) a comparison of these indices with the number of pups points to an increment of not less than 10% of the population. However, by the time the newborns become yearlings, the ratio between the additions and losses is equalized (Gol'tsev and Fedoseev, 1970).

Field characteristics. The adult common seal on Murman can be distinguished in external appearance from the ringed seal by its much larger size; slightly longer snout; small, almost black speckles on the skin; and the absence of a fairly broad monochromatically dark longitudinal band along the spine. It differs from the harp seal (gray-spotted animals) in the presence of light-colored ring-shaped patches on the back and the body flanks and the highly vivid dark color of the flanks in general; moreover, the harp seal does not come onto the coast. It is easily distinguished from the gray seal by its shorter snout, absence of a convex profile in the interorbital zone, and presence of light-colored ring-shaped patches on the dark-colored background of the skin. Unlike the bearded seal, the common seal is small and, moreover, spottiness is more sharply manifest and streak-like gaps visible.

The Far Eastern pagophobic seals are recognized by their habitat (encountered in the coastal regions which do not freeze as a rule) and their ability to inhabit the elevated sections of the coast at a distance of up to 25-30 m from the waterline (the larga is usually found right in the water), by their size (usually larger than the larga), by the broad somewhat puffed up snout, and by bright spotty coloration; quite

often, contrasting light-colored, predominantly distinct ringlets without blackish-brown fine uneven speckles are scattered on the monochromatically dark-colored background. The adult larga during residence on the ice floes (in spring) is confined in groups consisting of a female with pup and an adult male. Later, in the molting period, the seals form hards of dozens of animals. They differ in coloration from the ribbon seal and the bearded seal in a variegated, spotted pattern on the skin, from the ringed seal in fine speckles scattered randomly on a gray background on which
 274 the ringed pattern does not form a continuous grid or lattice, formed by the fusion of ringlets, as in the ringed seal. Moreover, the ringed seal is much smaller than the larga and has a relatively shorter trunk and snout.

In the beach rookeries largas are readily recognized by their close disposition, their movements (scuffles are frequent in the rookeries), and mainly from the racket they raise, especially at the moment of seizure, and their screams, which sound like a cacophany of barking dogs and bellowing cows (S. Naumov, 1941). The racket can be heard for distances of 2 km or more in quiet weather.

Unlike the larga, the island seal is quiet and almost does not raise its voice in the rookery. Only in the case of danger do the females signal the pups with guttural sounds resembling the "boom" of a bittern (Marakov, 1966*). It has been pointed out that the island seal lying on an isolated boulder jutting out not very high above the water usually lies with the head as well as the hind flippers held high, its silhouette resembling a boat with a high bow and stern (Marakov, 1966*). Further, the larga can also be seen on ice floes with raised hind flippers. (K.Ch.)

Economic Importance

The European common seal, being extremely few within our waters, is of negligible commercial importance. This seal is generally not caught at all on Murman. The pagophobic populations of the Kuril or island seals have no commercial prospects since their number is negligible, although the local people use a few of them here and there in Kamchatka and at some other places.

The larga commands considerable commercial interest. In fact, it is not the only one among our Far Eastern seals whose reserves, in most regions, are being exploited much below the population abundance. The larga has been practically of no interest to the state shipping industry in the Sea of Okhotsk from the early 1930s. It occupies the last and negligibly small position: in the Sea of Okhotsk in 1937 to 1939 its proportion

varied from 4.8 to 8.0% (average 6.5%) of the total catch; the bulk of the catch in these years (as also in the 1960s and 1970s) comprised the ringed seal, Pacific bearded seal, and the ribbon seal. Over two-thirds of the catch of larga came in the summer-autumn hunting season in the beach rookeries of Gulf of Sakhalin, Shantarsk Islands, and partly of Tatar Strait where 500 to 1,000 animals were caught annually. State hunting in the beach rookeries commenced in 1934, was quite irregular, and continued only up to the end of the 1930s in spite of the larga being readily accessible. Thus, in 1934, some 1,500 animals were caught in 22 days (Tikhomirov, 1966). The catch from 1937 to 1939 was high although apparently uneven. Hunting was not restored in subsequent years.

In spring, the main season of hunting using ships among drifting ice floes in the western regions of the Sea of Okhotsk, the larga accounted for 1.3 to 2.3% (average 1.8%) of the total catch from 1937-1939 (Pikharev, 1941). The reason for this low representation of the larga lay in the characteristic dislocations of its major concentrations on the ice floes in the Sea of Okhotsk as also in its behavioral characteristics. In the early spring the whelped and lactating mothers with pups as also the adult males are concentrated in the Sea of Okhotsk among compact frozen ice
 275 floes that are difficult for ships to penetrate. Later, however, when the ice floes become thin and the reproduction period has concluded, the largas gather in the molting rookeries, which are unfavorable for hunting for the sole reason that it is difficult to approach the cautious animals: at the very first rifle shot all the animals disappear into the water where they are inaccessible to the hunters.

In the early postwar years hunting of larga in the Sea of Okhotsk intensified perceptibly as a result of enlarging the fleet and the region of its activity. Thus from 1954-1958, the annual catch went up to 3,100 animals, or 4.3% of the total during intense seal hunting. In the next spurt of activity the specific proportion of the larga rose further: from 1959-1963, an average of up to 6,000 animals was caught (Fedoseev, 1966) or 6.8% of all the seals killed in these years.

From the very beginning of the 1960s, hunting by means of ships occurred in the Bering Sea too, although the larga was caught there in the smallest numbers compared with other seal species: in the early years its proportion in the total catch was only 2.1% in spite of the fact that its population was sufficiently large to support a higher level of kill and to reduce the pressure on the other seal species.

In the early half of the 1960s, the total catch of the larga in the entire Far Eastern basin, including hunting by the local people, went up to 10,000-15,000 animals. Its proportion in the seals killed by hunting

using ships did not, however, exceed 9.4% in the best years (Tikhomirov, 1966a).

Some intensification of larga hunting with reduced killing everywhere of the Pacific bearded seal as well as the ribbon seal and partly the ringed seal is one of the possible methods of rational utilization of the seal resources using ships in the Far East. Intense hunting of the larga would evidently reduce the damage caused by these seals to the salmon reserves. As already pointed out (p. 339), the larga consumes and damages quite a large quantity of Siberian salmon, humpbacked salmon, and other even more valuable types of salmon, which serve as food for the larga in summer. The largas gather in large herds in the fore-estuarine sections, directly in the estuaries, and right in the lower courses of rivers during the period of arrival of salmon for spawning and do not so much consume them as damage them (especially when the fish are abundant), by selectively nipping small bits of flesh along the spine. This adverse role of the larga cannot be ignored, at least at places where fish catching, preparation, and processing have been organized. The Canadian government offers a handsome reward for killing even one seal (*Phoca v. richardi*). In the most important salmon rivers of British Columbia, over 12,000 seals were destroyed over a 10-year period, from 1939 through 1948. From 1941/42 through 1946 alone, some \$32,000 were spent for the destruction of 10,000 seals (Fisher, 1952). The loss inflicted by the seal to the fishing industry in Alaska, especially in the Mednaya River region, is nearly 2-3% of the total salmon catch here (Imler and Sarber, 1947). In the spawning rivers of British Columbia during the arrival of salmon, these fish constitute about 30% of the food of seals (Spalding, 1964).

The technique of hunting using ships is generally as follows. Motor schooners capable of negotiating among ice floes set out with several motorboats on board, which are dropped in the water in the region of hunting as soon as a sufficiently large number of animals is sighted. The ship heaves to and each boat (with a crew of three in white masks) is assigned a particular direction. The ship maintains radio contact with the motorboats. The teams must not only not lose track of the sighted animals, but also attempt to approach them within rifle range while maneuvering among the ice floes. Depending on the situation, the boats move far away from the ship for several hours or even the whole day. The skin with blubber is recovered from every killed animal while the rest of the carcass (skeleton with musculature) is only carried if space permits.

276 During lactation close approach to the larga depends exclusively on ice conditions. If the ice is dense and the motorboats cannot negotiate, the ship approaches the animals. The larga can be shot directly

from the ship or experienced hunters climbing overboard and jumping from one floe to another can approach the animals singly. Instinct holds the suckling mother close to her pup in spite of fright. The adult male in the proximity of the female with a pup is usually the prized trophy of the hunters. Killing of isolated young (immature) larga dispersed on the ice floe poses no problem. The situation changes, however, at the end of the lactation period. Then hunting becomes quite difficult.

Until comparatively recently, the larga was killed even in the beach rookeries. For this purpose, 15 to 20 hunters in two boats dropped from a ship in the vicinity of a rookery would set out for it taking care not to frighten the animals. Landing away from the rookery and armed with clubs, they would approach the animals as closely as possible by crawling under cover, ready to attack at a signal from the leader. This method was not always successful but often yielded over a hundred animals. In a successful hunt, from the viewpoint of the hunters, 5-10% of the animals in the rookery could be killed thusly, or 500-1,000 animals throughout the autumn hunting season (Pikharev, 1941). But not all autumn hunts for the larga in rookeries were successful (sometimes the frightened animals escaped before the hunters could reach them); moreover, the killed animals had to be dressed before high tide as otherwise the waves carried it away and recovery was difficult.

On the open coasts, where it is practically impossible to approach the rookery, nets are more commonly used to catch the animals. With the onset of darkness, one group of hunters in a boat carrying a sweepnet comes within 50-75 m of the rookery and carefully spreads the net over this area. An auxiliary group of hunters, waiting in another boat at some distance from the rookery, then approaches the net-covered site and both parties draw the ends of the net toward the coast. Between 200-250 seals were caught in one such net in the estuary of the Moroshchechnaya River (western Kamchatka) (Tikhomirov, 1966a).

Typical methods of killing the larga in the autumn rookeries are practiced in Tauisk Bay by the Orokhets. On the open rocky coasts the hunters make a preliminary hideout near the rookery, using for this purpose a boat priorly cast off near the site. As soon as the seals have become habituated to the hideout, the hunters, taking advantage of high tide, when the animals abandon the rookery, gather in the hideout and wait for the animals to return. Allowing some time for the animals to settle down, the hunters then pounce with clubs and quickly kill as many seals running panic-stricken into the water as possible (Tikhomirov, 1966).

The Sakhalin Gilyaks have long adopted a very unique but highly ineffective method, using a boat and a long (4.0-4.5 m) flexible pole to which a large ski-like float with a harpoon is attached. Dropping this equipment in the water, the hunter attempts to take it to the closest diving seal and, when successful, pierces the animal with a powerful thrust of the harpoon (Nikol'skii, 1889).

In various sections of the vast Far Eastern coast, other hunting methods are known but none are specific for killing the larga. Two methods are very common and extensively used. One is practiced from the end of summer and in autumn. The hunter crawls up to the seal from the coast, shoots it, and rapidly drops a light boat to catch the wounded animal; quite often, however, the seal drowns. In spring the hunters from the coastal villages (mostly from the Bering Sea area) come out in large
277 motorboats and seek the animal among thin coastal ice in quite the same way as done by the hunting parties from a ship in the more pelagic regions.

The skin of the newborn larga (white pup) up to five days of age does not command the same high price as that of a harp seal (greenish-white pup) or some other seal born on the ice. The skin of the larga can be used in collars, caps, and other fur goods in a natural state or dyed. However, the number of such skins produced in the early spring hunting season is negligible. Given the prevailing hunting conditions, especially in the Bering Sea, it is difficult to say whether the hunters in one ship can catch over 200 undamaged skins of white pups of this species during the season.

The skins of molted pups (killed somewhat later) and juveniles (one to two-three years of age) with a more beautiful, brightly spotted color and relatively thin skin are of much greater value. Because of these qualities and also because of the relative rarity of such skins, the larga has long received particular attention from the coastal people, especially the Chukchis, Koryaks, and Eskimos. They use these skins for making dresses and generally for more delicate work, in particular for fashioning women's apparel.

Until quite recently (1960s), the prevailing fashion for seal skin articles such as caps, jackets, cloaks, shoes, etc. put the seal skins, especially of young ones, in high demand in the fur market. The fashion for short, rigid furs of natural color necessitated catching not the white pups, but the molted pups and the older juveniles. This is all the more rational as such skins are more accessible and hunting is not restricted to the brief spell during which the pups sport the neonatal embryonic fur. Even the skins of the adult larga are perhaps suitable for this purpose through

their hair coat is slightly sparser and more rigid, the color less attractive, and the hide considerably thicker and heavier.

The quantity and thickness of the subcutaneous adipose tissue varies according to the season and the age of the animal. Newborns are almost devoid of it but accumulate a 3-4 cm thick fat layer (together with the skin) in the short lactation period and weigh roughly 15 kg (also with the skin). The skin with the subcutaneous fat (blubber) of animals in a transitional age weighs 15-25 kg. The thickness of the fat layer in adult animals in spring differs little from that of the immature animals but exhibits sharp seasonal changes. The weight of the blubber of the larga in spring (especially after lactation and mating) averages 20 kg; it doubles to 40 kg by autumn (Fedoseev and Shustov, 1964*).

The meat of the larga is used as required by the trade. The demand for it has been increasing year by year with the expanding animal farms, particularly in the local coastal collective farms of the Far East. The meat with bones of a young larga weigh 15-20 kg and of semi-adult and adult animals 35-40 kg.

Rules governing the utilization of the Far Eastern marine animal resources have not been properly drawn up to date. This applies to the larga also, although there is no need for special controls on its hunting. However, the need to reorganize the hunting activity is quite considerable. Any seal providing fur (and hence the larga too) deserves the same attention as the fur seals.

There is also need for special supervision over the utilization and study of the less abundant island (pagophobic) seals on the Kuril Islands, Commander Islands, and along the eastern coast of Kamchatka, all the more since these seals, as far as is known, do not affect the fishing industry. (K.Ch.)

Subgenus of Harp or Greenland Seals

Subgenus *Pagophilus* Gray, 1844

HARP OR GREENLAND SEAL

Phoca (Pagophilus) groenlandica Erxleben, 1777

- 1777. *Phoca groenlandica*. Erxleben. Syst. Reg. Anim., p. 588. Greenland.
- 1778. *Phoca oceanica*. Lepechin. Acta Academ. Petropol., I, p. 259, Tables 6 and 7. White Sea.
- 1785. *Phoca semilunaris*. Boddaert. Elen. Anim., p. 170. Greenland, Iceland.
- 1811. *Phoca dorsata*. Pallas. Zoogr. Rosso-Asiatica, I, p. 112. White Sea. (V.H.)

Diagnosis

These are relatively large seals. The body length of the adult reaches 2 m (even more in some cases) up to tip of tail along the dorsal surface (*Lc*). The adult skull is 185-240 mm long. The color of the hair coat varies (depending on the age and to some extent on the sex) from spotted gray (with haphazard but not very densely scattered dark, mostly angular patches in a gray background) to a bright contrasting "wing pattern" with two very large highly elongated dark-colored, almost black patches, sharply prominent in the light-colored background. This "wing pattern" is disposed symmetrically on both sides and the anterior tips converge on the back. In the final dress of the animals the color of the anterior portion of the head is the same as that of the "wing pattern".

The skull is quite massive, with thick bones. The upper and lower processes of the posterior edge of the zygomatic bones are nearly equal in length; the bony nasal septum in the choanae reaches the posterior edge of the bony palate. The palate has no significant notches but a central prominence, turned backward, is usually seen. The bony lobe of the external auditory meatus is genuflexed forward. Molars and premolars (except the first) have two roots while the crowns, especially of the lower jaw, bear well-developed accessory cusps. (K.Ch.)

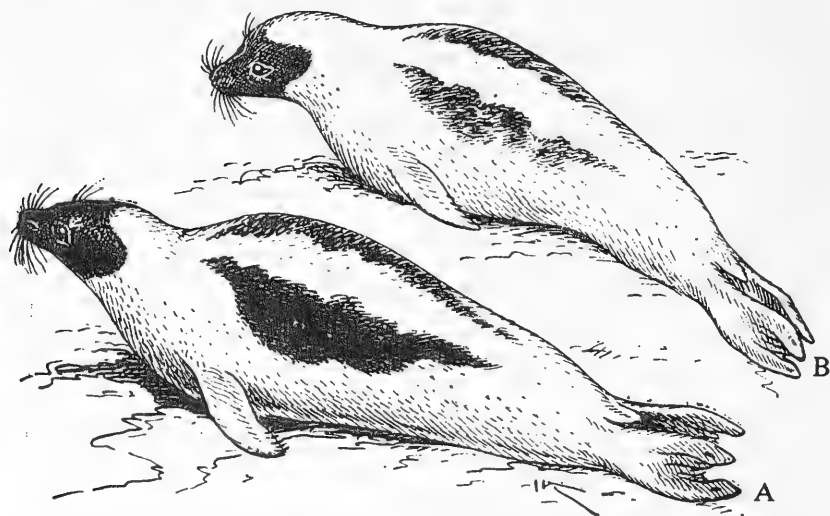


Fig. 160. A—male harp seal, *Pagophilus groenlandica*, with the final color of the "wing pattern"; B—adult female harp seal in the "semiwinged" phase of color (incomplete pattern of the "wings" covered in sparse spots) (figure by N.N. Kondakov).

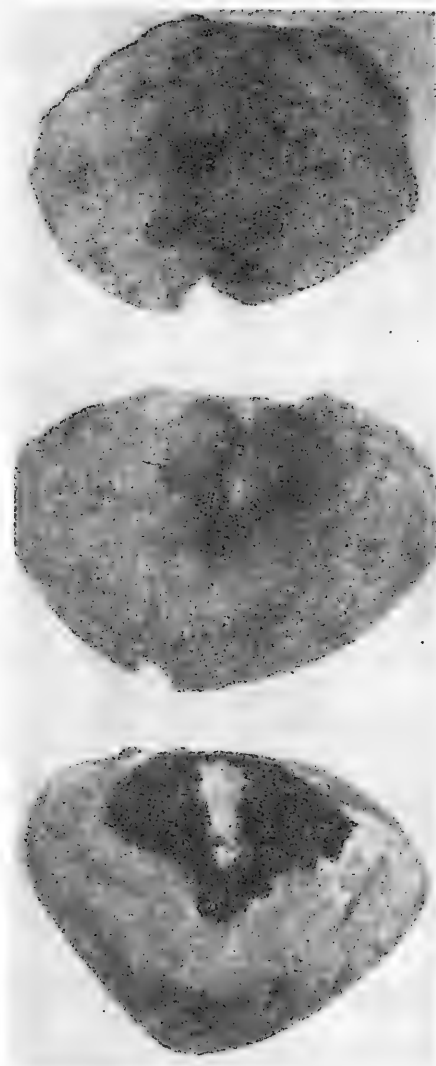
Description

The external appearance is typical of seals of the genus *Phoca* but the adult animals are perceptibly larger than their counterparts in other species of this genus. The body is almost perfectly streamlined and its hydrodynamic characteristics improve with growth (Alekseev, 1966). The claws on the fore flippers are quite massive, blackish-gray, with a distinct transverse rib formation among adults; on the hind flippers these age-related bands or segments are less prominent or distinct. The length of the digits on the fore flippers decreases successively from the first and the second (which are nearly equal in length) to the fifth.

The whiskers are dark gray, flattened, with wavy edges. The labial whiskers are usually disposed in 7 rows; each side of the lowermost row most often has 7 (6 to 9) whiskers, the second to the fourth 9-10 (8 to 11), the fifth 4-9, the sixth an average of 4, and the last an average of 2. Sometimes a lone whisker is seen above the seventh row. The labial whiskers total 46-47 on each side. The supraorbital whiskers number 279 most often 3 each but vary generally from 1 to 4. As a rule, there are two whiskers around the nostrils on each side (Yablokov and Klevezal', 1964).

Two types of hair coat are common among pagophilous seals. These are successively the neonatal (juvenile, white) and the definitive form acquired on shedding it. The first consists of tender wavy fur hairs set very densely in tufts to form luxuriant and concomitantly dense and long creamy-white fur. The definitive hair coat of the harp seal in structure, strength, and notable slant (pile) is the same as in the other seals. It consists of uniformly distributed tufts, usually comprising three categories of hairs: guard hair (12.5 mm long), intermediary 1-2 (6.2 mm long), and 4-5 fine and wavy fur hairs (5.5-7.7 mm long). These are disposed in a definite sequence; intermediary hairs anterior to the fur hairs and the guard hairs shifted forward even more, covering the rest of the tuft constituents. A 1 cm² area has 1,700 such tufts with a total number of about 12,000 hairs (Bel'kovich, 1964).

The color of the hair coat varies greatly with age (Fig. 161) and the final wing pattern is highly typical and contrasting: one large, long, distinctly contoured, vivid brownish-black patch each on the right and left sides of the trunk on a very light, white, almost pure white, or slightly silvery background. The anterior tips of the patches fuse roughly in the zone of the scapula on the dorsum and with a slight divergence extend backward and downward along the flanks; the patches enlarge perceptibly in this process with a slight crescent-like form in the midportion. Later, they gradually narrow and disappear in the sacral zone near the



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Fig. 161. Main changes in age-related skin patterns among harp seals. Top to bottom: gray form (1-3 years old); transitional phase of female (average 3-5 years old); and final coloration, i.e., the winged form (5 years and above) (photograph by R.Sh. Khuzin).

base of the tail. On a flat skin they resemble a typical horseshoe or are somewhat lyre-shaped. The head almost up to the neck, ear openings, and up to the anterior front is the same color as the "wing pattern".

Such a coloration is acquired by successive transformation which proceeds slightly differently among males and females. The color of the first definitive hair coat (juvenile) acquired on shedding the white coat (neonatal) consists of a light ash-gray main background (quite often, slightly darker on the upper side) and usually a few dark gray or brownish-black spots. These spots vary widely in number, are randomly scattered, often in small groups with small and very large ones intermixed, sometimes with fairly angular outlines. This is the color of the young seal (one to three years).

The white coat at birth (neonatal) in males and females is altogether identical (see above). The infantile coloration succeeding it on shedding of the white coat is also typical with no specific differences between males and females.

The transitional spotted gray color is sported, almost without change, for several years in spite of annual molt. Its shortest life occurs in males: less than half the generation has it for five years and not more than a quarter for six years. As far as is known, older males with a spotted gray coloration do not exist. Females, however, are seen much longer in this infantile coloration, i.e., up to 10 or more years of age; even at eight years, their proportion can be 50% (Khuzin, 1964). Stray spotted gray seals are encountered from time to time even among 14- or even 17- or 20-year-olds (Potelov and Mikhnevich, 1967).

The next transitional phase of coloration is the formation of an incomplete "wing pattern". It reveals a mixture of the original features, i.e., spotted gray (or grayish) and the final "wing pattern".⁸⁸ The life of this stage too varies in males and females. Only the very beginning of this phase is generally similar in both sexes.

Very indistinct, highly diffuse darkening is seen initially at the site of the future "wing patterns". Their coloration is most vivid on the upper (internal, or dorsal) edge which is very distinct and sharply demarcated from the gray background. The "wing pattern" rudiments turn increasingly pale toward the lower lateral edges as though faded and gradually merge with the light gray main background of the body flanks and underside. This shadow of the wing pattern is covered at places by stray, rare,

⁸⁸ Our special literature used to refer to such 20-year-old females as the "second phase, with gray wings" (N. Smirnov, 1927) but this phrase was later replaced by the term "semi-winged," first applied to males in which the pattern was not fully formed (Chapskii, 1952).

small spots that are new and bright as well as the remnants of infantile coloration. After the next molt, the "wing pattern" appears more distinctly in some while the features and the color vividness vary little in others and, as before, remain more distinct only along the upper edge and are covered with spots.

At this stage, sex-related differences appear in the very nature as also the tempo of color variations. In the semiwinged phase with an incompletely formed "wing pattern," the color transformation process is usually quite delayed among females. This age-color group commencing from the first five or six years (although relatively few in these generations⁸⁹) constitutes in succeeding years a perceptible proportion of almost up to two-thirds of the generation. Even among 17-year-old females, the number of semiwinged animals is obviously quite large. It is quite possible that a significant number of females never attain the final "wing pattern" phase but remain in the "semiwinged" coat to the end of their life (Khuzin, 1964; Potelov and Mikhnevich, 1967). Most females nevertheless reach the final color earliest at 6-7 years of age (roughly 10%
281 each of the animals in these age groups). At 10 to 17 years of age the number of females with a "wing pattern" increases perceptibly to around two-thirds of the generation.

Detailed descriptions are not available of the successive color gradations on transition from the semiwinged to the winged pattern. It can only be assumed that this transition is quite simple and sharp since the first of the youngest females with a "wing pattern" are just a year older than the first of the animals with a semiwinged pattern.

It therefore appears that some definite quantitative proportions of females of all coloration phases exist simultaneously in the six- to 14-year-old generations although the representation of the spotted gray variety is the least, semiwinged more (one-fourth to one-third), and the winged variety about two-thirds.⁹⁰

The transitional coloration among males is characterized by some specific features. This transition covers only three groups of ages from five to seven years while seals with the full "wing pattern" are also seen in these groups. It may therefore be assumed that the transition from

⁸⁹ According to some authors (Khuzin, 1964), the females acquire the semiwinged pattern coloration at six years of age; according to others (Potelov and Mikhnevich, 1967), however, this type of coloration is seen among 10% of even three-year-olds.

⁹⁰ Some differences are noticed in these proportions among various populations. The White Sea females preserve the infantile (spotted gray) coloration only up to 10 years of age and the semiwinged pattern up to 16 years; the corresponding ages among the Jan Mayen females are 15 and 22 years; a similar lag of color transformation is also characteristic of the Newfoundland females (R.Sh. Khuzin).

the spotted gray to the final phase is extremely short among males and often the intermediate semiwinged phase is bypassed. Nevertheless, the latter phase in turn can be subdivided into a few stages (Chapskii, 1967).

The first stage is the very dark "wingless" type: the dark spots are so densely scattered that they cover the main background almost wholly so that the "wing pattern" is not visible; such animals look like a black silhouette from a distance.⁹¹ Animals with a faintly identifiable "wing pattern," lusterless like a dim shadow, can be seen in this group. The ages of the males sporting both color variations are wholly identical: roughly 40-43% each of four- and five-year-olds and 15-20% of six-year-olds.

282 The second stage, forms with a "semiwinged pattern," is distinguished by fully developed contours of the lower edge of the "wing pattern" and considerably lighter but densely spotted main background (except for a dorsal, very dark clearance between the "wing patterns") and even more vividly colored snout (Fig. 161). The age of such males is predominantly six years but even five-year-olds (possibly even four-year-olds) are encountered in this stage.

The third stage of coloration, spotted "wing pattern," is the final phase with a sharply distinct posterior boundary in the dark coloration of the head but still with quite a large number of spots or dabs which are generally dull and scattered in the bright main background. Such males are close to the forms with a "semiwinged pattern" in age: more than one-half of them are six-year-olds, about one-third seven-year-olds, while the five-year-olds constitute roughly one-seventh.

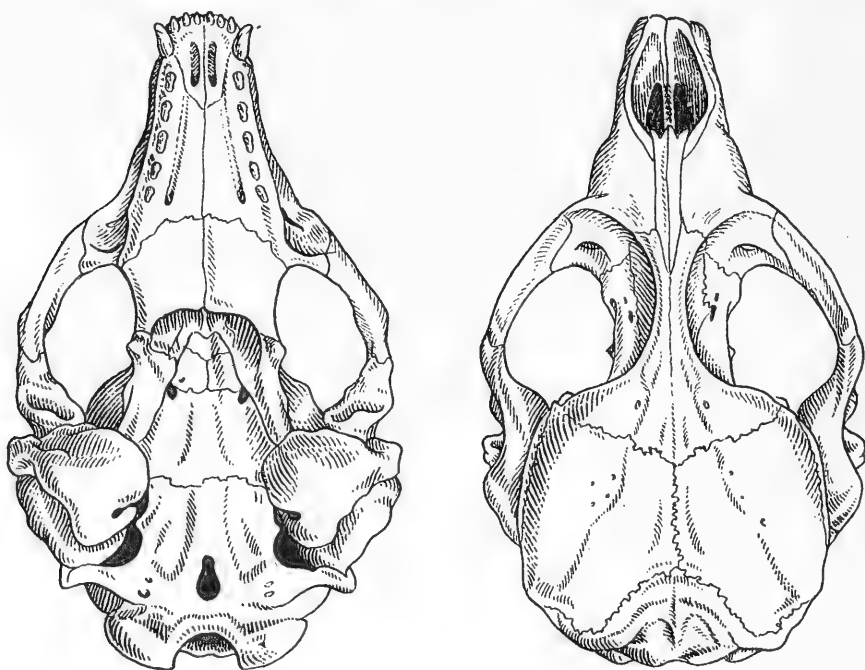
Thus the transition from infantile to final adult coloration among males occurs over three years (from the fourth through the sixth inclusive). All the males do not necessarily undergo the intermediate stages of coloration. The majority enter the "winged" phase, either totally bypassing the intermediate phases or passing through only one or two of the later stages. Thus the fourth year is the last year of the infantile period in which all the males still sport the spotted gray coloration (or gray animals), and the fifth year is the first year in which one-fifth or one-third of them acquire the final wing coloration. All the males develop the wing pattern by the eighth year (Potelov and Mikhnevich, 1964, 1967; R.Sh. Khuzin; Chapskii, 1967).

The maximum range of individual color variation is noticed in the period of growth and formation of final coloration. It is high among animals preserving the infantile type of coloration as also among mature females of a much younger age and partly also among males in the transitional "semiwinged" phase. Among the younger animals in the

⁹¹ White Sea hunters call them "ogar," "salovar," etc.

population bearing a spotted gray skin, it is difficult to find animals in which the disposition, form, density, and even the color of the spots, and partly the main background are totally identical. There are very light-colored animals, sometimes with dense variegated spots and sometimes with extremely few spots; there are several variations between these types. Among the females with a prominent "wing pattern," their contours, superimposition with stray spots, and pattern of spots vary markedly. Among the males in the transitional phase to the final form of "winged" type of coloration, all possible variants of dark aberrations and spot patterns are encountered.

The skull (Fig. 162), seen from above, is somewhat similar to that of the large larga (*Phoca vitulina largha*) but the zygomatic arches do not protrude markedly into the sides: the width at the zygoma in adults is only slightly more than that of the cranium measured⁹² between the mastoid processes. It constitutes 90-110%* ($\bar{x} = 102\%$) of the mastoid width



283 Fig. 162. Skull of the Greenland (harp) seal, *Phoca (Pagophilus) groenlandica* (figure by N.N. Kondakov).

⁹² The craniometric data are from the author's materials with some corrections by R.Sh. Khuzin (1967a*) marked with an asterisk.

or about 55.5% of the condylobasal length. The interorbital constriction varies from 9.5 - 13% of the mastoid width. The width of the rostrum (at the level of the upper canines) varies from 23 - 36% ($\bar{x} = 29\%$)*. The length of the facial portion (up to the uncinat processes of the pterygoid bone) is roughly one-half (\bar{x} not over 52%) of the condylobasal length.

283 The basic skull features of the species mainly occur in the basal side of the axis of the skull and also in the structure of the lower jaw and the zygomatic bones. The midportions of the posterior edge of the bony palate are shifted relatively far back and are fairly at level with their lateral sections without forming a distinct palatal notch; a reverse situation is also seen quite often when, at the end of the median suture, a perceptible inverse projection is formed. This formation is promoted by the longitudinal bony septum in the choanae reaching the posterior edge of the bony palate and quite often extending slightly beyond. In such cases the rear section of the palate is in the form of two highly flattened fused arches. The zygomatic process of the temporal bone is turned forward and not perceptibly enlarged. The choanae are low (height roughly one-half their width).

The tympanic bullae are roomy, with quite complex contours, and rounded-triangular in the horizontal plane. The angularity intensifies somewhat with age. Their width (together with the lobe of the auditory meatus) is greater than their length and averages slightly less than 20% of the condylobasal length. The bony lobe of the external auditory meatus is massive and genuflexed forward. The jugular processes in most cases project above the skull surface and are bent backward. The uncinat processes are not bent outward. The nasal bones, constituting about one-fifth of the total length of the skull, are wedge-shaped with a highly enlarged anterior tridentate margin. The nasal processes of the maxillary bones extend along the nasal bones usually for not less than one-fifth the length of the latter. The sagittal crest is almost absent while the occipital crest is not strongly pronounced. The subcondylar process is well developed in the lower jaw and is perceptibly incurved.

The molars and three posterior premolars and the molar on the lower jaw bear well-developed accessory cusps spread fanlike on both sides of the main cusp (one each in front and, in most individuals, two each at the back). In the corresponding teeth of the upper jaw, the anterior accessory cusp is poorly developed (altogether absent in most premolars but quite often preserved in the molar).

Skull differences between males and females are not striking but become distinct on statistical processing of the data. The upper contour

of the skull profile in the frontal portion among males is in the form of a perceptibly curved line; this curvature is far less noticeable among females.⁹³ A paired fold on the lateral fronto-sincipital surface from where the temporal muscles originates is more intensely manifest among
 284 the males. The bony nasal septum in the choanae is more developed among males while it is often incomplete (with a notch on the posterior margin) among females. The anterior margin of the nasal bones in males has very long lateral teeth while the median teeth are more often the longest among females. The width of the rostrum at the level of the canines in males is 26-33.5% (M 30%) of the width at the mastoid and in the females 23-32% (M 27%). The width at the zygomatic arches quite often slightly exceeds that at the mastoids in males but not in females. Statistical processing of the data revealed that these and several other craniological values are somewhat higher in males than among females. In general, the skull of the male is perceptibly more massive and heavier.

Age-related variability of the skull is very high. Along with an increase in its dimensions and weight, an extremely distinct age-related feature is the development of its crests and the general surface relief of the cranium. Among newborns, its dorsal surface has an almost wholly smooth fronto-sincipital obtuse area angularly turned toward the nose bridge. The sides of this "angle" from where the paired temporal muscles emerge are even less prominent. With age, they become increasingly contoured and are displaced toward the midline. As a result, the anterior width of the area steadily decreases and the anterior angle becomes increasingly acute while the marginal folds formed are transformed almost into a crest and come increasingly closer. Concomitantly, the very faint rugosity observed along the lambdoid suture only among the newborn, develops into a sharp crest with an overhung pointed dentate cornice in the adult.

The age-related changes of other craniological characteristics are less striking but are readily discernible in statistical processing of the data. The most significant are the following:⁹⁴ (1) the posterior margin of the bony palate in the newborn usually has slightly more concave contours, sometimes with a mark on the notch, the latter filling up during growth and even transforming into a reverse fold in the midportion; (2) the base alone of the bony nasal septum in the choanae in most young animals reaches (not invariably though) the posterior margin of

⁹³ This is not a characteristic of the race (N. Smirnov, 1929) but is of sex-related secondary importance (Plekhanov, 1932*; Chapskii, 1952; and others).

⁹⁴ Data pertain to the White Sea population.

the bony palate; hence, there is an angular notch along its height. In adult and older animals, however, it is not only filled up but its upper portion even emerges beyond the margin of the bony palate; (3) the subcondylar process of the lower jaw is fully developed (i.e., reaches the vertical of the condylar process), also only in the adult; (4) the tympanic bullae in young animals are relatively more swollen, with a smoother, round surface, and more simply contoured than in adults. Their position is more firmly fixed with age; in the young they may be disposed anterior to the rear crest of the articular fossa while they are invariably posterior to the latter in the adult; (5) the flexure of the upper profile in the zone of the nose bridge becomes apparent with age but is absent in the newborn; (6) the premolars and molars which have already emerged from the alveoli are disposed in young animals almost without gaps, their edges often touching each other and sometimes even slightly extending beyond the crowns one behind the other. With age, gaps arise between them as a result of the elongation of the jaws and become widest by the time total maturity sets in. Tooth wearing becomes perceptible only in very old animals; in males and females with the "wing pattern," the accessory cusps of the crowns become worn to a variable extent; in much older animals, even the main cusps are highly worn down but the crowns are not usually completely worn down. The cusp and partly the side of the canines are worn but fully worn down canines are almost never found. The incisors in adults are also quite often highly worn down; moreover, with increasing age, some straightening of their upper row is noticed (the incisors are set anterior to the margin in an even file while they are arranged in a slightly semicircular fashion in the young); and (7) the apex of the nasal bones (the depth of their wedging into the frontals) changes with advancing age in the following manner, as a percentage of the total length of the nasal bones:

	<i>Mean</i>
Up to one month	41.5 (n = 28)
From one to three years	43 (n = 20)
Males with "semiwinged pattern" (five to six years old)	44 (n = 12)
Males with "winged pattern" (adults)	44.5 (n = 13)

The skull proportions too vary with age, especially the ratio between total skull length and width of the cerebral portion (the skull becomes increasingly longitudinal).

The width of the skull in the region of the zygomatic arches increases steadily (toward the time of attaining maturity, it is comparable to and even slightly exceeds the mastoid width). The rostral width (level of the

canines) expressed as an average percentage of the mastoid width reveals the following course of changes:

	%
Age up to one month	22.7
One-year-olds	24.5
Two- and three-year-olds	26.2
Mature animals	28.6

In young animals the rostral portion is not only noticeably narrower, but also considerably shorter and lower than in adults. The cranium reveals a reverse tendency (in the young it is relatively more swollen; the length of the tympanic bullae as a percentage of condylobasal length decreases from the first year to old age by 4%), etc.

The range of individual variation in craniological features is quite significant even among such animals as reveal systematic changes sexwise. Thus the index of rostral width which points to a harmonious increase from one age level to another in animals of nearly the same age (for example, in males with the "winged pattern") varies from 26 to 34 while the index of the interorbital constriction varies from 10.5 to 16.5, index of the width at the zygoma from 98 to 109.5, etc. Skull elements such as length of the nasal bones, shape of their anterior notch, contours of the posterior margin of the bony palate, etc. also vary.

The body length of the adult, fully grown. White Sea males measured between tip of nose and tip of tail in a straight line (*Lcv*) is 155-188 cm. However, the length measured along the dorsal surface (*Lc*) is 169-205 cm. In the White Sea adult females, *Lcv* varies from 153-188 cm and *Lc* from 167-202 cm⁹⁵ (Khuzin, 1963; M.Ya. Yakovenko).

The length of the os penis in the adults averages 160 mm.

The total weight of the White Sea well-fed adult can reach a maximum of 164 kg and that of the skin with blubber removed by the commercial method up to 69 kg (Yu.I. Nazarenko).

Weight of heart 600-960 g; liver 1,500-2,400 g; total length of the intestine at 1,900-2,870 cm exceeds the body length of the adult 13.6 times (Yablokov, 1963).

The condylobasal length of the skull of adult males (37 animals from the White Sea) was 199.8-235.8 mm (\bar{x} = 217.0); zygomatic width 107.0-142.0 mm; mastoid width 113.0-133.3 mm (\bar{x} = 122.4); width of

⁹⁵ 229 cm in an extraordinary case.

the snout above the canines 30.0-43.5 mm (\bar{x} = 36.2); and the smallest interorbital width 8.8-21.0 mm (\bar{x} = 15.0).

286 The condylobasal length of the skull of adult females (27 animals) from the White Sea was 193.0-223.2 mm (\bar{x} = 210.6); zygomatic width 105.3-130.3 mm; mastoid width 11.4-138.0 mm (\bar{x} = 119.5); the rostral width at the canines 28.6-40.0 mm (\bar{x} = 32.8); and the smallest interorbital width 9.1-16.0 mm (\bar{x} = 12.7) (Khuzin, 1963, 1967).

The reliability of the craniological differences between males and females is also confirmed by statistical variance analysis (t more than 3 or 2). The differences are reliable in all the populations: condylobasal length, width at level of canines, and smallest interorbital width (Khuzin, 1963; Yablokov and Sergeant, 1963; Khuzin, 1967). The difference in the index of rostral width (as percentage of the condylobasal length) is reliably or significantly higher in males than in females (Khuzin, 1967).

Within the territorial waters of the USSR, the overall dimensions and craniometric values of the harp seal reveal no geographic variation since our waters are host to animals of one single population that reproduces in the White Sea. The breeding center of the other, i.e., the Jan Mayen population, nearest to the White Sea population, is separated by over 2,000 km from the breeding site of the latter and the transgressions of Jan Mayen animals into our waters are very rare (see p. 407). The differences between the Jan Mayen population, which is isolated from the White Sea population spatially and in breeding sites, are nevertheless very minor (see pp. 387-390) although the Jan Mayen population is classified as a special group. (K.Ch.)

Taxonomy

Pagophilus Gray may be regarded as a special subgenus within the genus *Phoca* s. l., *Ph. groenlandica*. The seals of *Phoca groenlandica* differ more from those of the subgenera *Pusa* and *Phoca* s. str. than from species of the subgenus *Histiophoca*. The harp seal has several characteristics proximating it with *Histiophoca*, the most important being the common final coloration of the hair coat, i.e., alternation of large sections of very dark and bright coloration. Some craniological features too are similar: (1) relatively poorly developed and shortened lower posterior process of the zygomatic bones, the length of which often does not exceed or only slightly exceeds the length of the upper process; (2) forward projection of the temporal bone without enlargement on the anterior margin of the terminal section of the zygomatic process; and (3) some similarity in the shape of the posterior margin of the bony palate and in the development of the compact longitudinal septum in the choanae; etc. There are elements of similarity in ecology also: the seals of both

these species are confined to drifting ice floes without emerging, as a rule, onto the coasts, lead a pelagic mode of life, and perform fairly significant migrations.

Based on these elements of similarity, an attempt was made (however, not supported by later authors) to combine the harp seal with the ribbon seal into one genus, *Histriophoca* (N. Smirnov, 1929, 1935). Much later, it was proposed that these species be combined (at the level of monotypical genera) into a subtribe, *Histriophocina* (Chapskii, 1948, 1955). These species figure in different genera in several contemporary works (Scheffer, 1958; king, 1963*; Chapskii, 1963).

The similarity between these genera is also seen in the number of cartilaginous rings of the trachea (average 43), relative length of the intestine (13.6 to 14.4 times the body length), variation coefficient of the weight of some internal organs, and relative similarity of the number of labial whiskers (Shustov and Yablokov, 1967).

A greater generic proximity between the species compared, than with any others, is also detected in the response to precipitation (V.I. Borisov). The evolution of the harp seal from a common ancestor with the ribbon seal is hardly debatable, but the divergence of these species should be placed not in the Quaternary period (Davies, 1958), but in a much earlier period, probably the Pliocene.

287 There is a view (Winge, 1924, 1941) that the harp seal is more advanced in some respects than the other species, especially subgenera *Phoca* s. str. and *Pusa*. The more advanced evolutionary features of this branch are seen in the elongation of the bony palate (also due to the equalizing of its posterior margin) and in the growth of the longitudinal bony septum in the same direction (up to the posterior margin of the bony palate).⁹⁶

Geographic Distribution

The subarctic and arctic expanses of the Atlantic Ocean and parts of the northern Arctic Ocean adjoining the eastern fringes of the Atlantic Ocean.

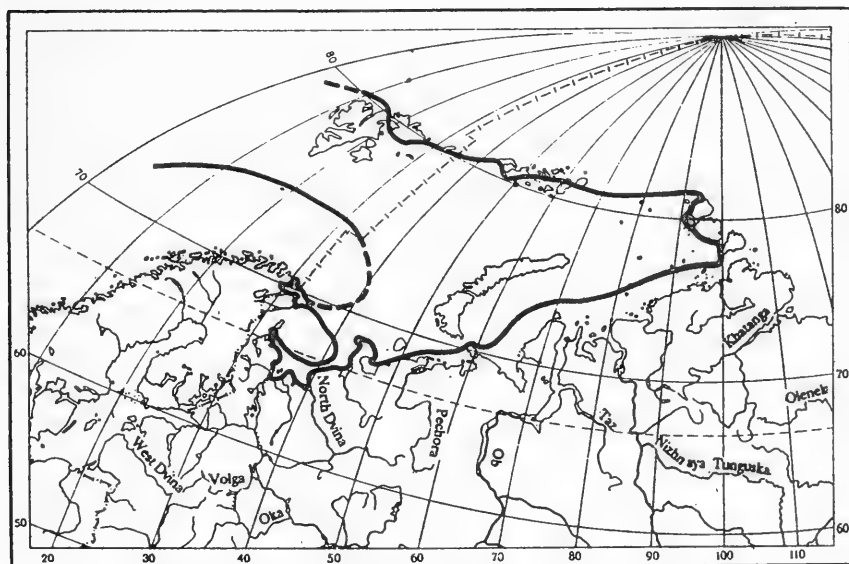
Geographic Range in the USSR

Constitutes the easternmost part of the general range (Fig. 163). The range of this species within our territorial regions and the adjoining international waters covers the entire coastal belt of the Barents Sea

⁹⁶ Such an interpretation of the structural features the skull is somewhat debatable in the light of some new facts (Chapskii, in litt.).

along Murman from the boundary with Norway to the White Sea inlet, including all the bays and straits, even those penetrating deeply inland, such as the Kola and Motovsk. Farther east, the range encompasses the entire Kanin-Kolguyev shallow-water zone, Cheshsk and Indigsk bays, the mainland portion of the sea to the north and northeast of Cape Timansk of St. Nos, extending along the Timansk coast toward the Pechora Sea from its northwestern, northern, and northeastern regions right up to Vaigach itself. However, the southern and southeastern continental sections of the mainland sections of the Pechora Sea bound roughly by a line traversing from the Russkii Zavorot to Yugorsk Shar, including the latter, and also the coastal waters of Dolgii Island, and all other expanses south of the above line fall outside the limits of the range.

288 Farther north, the region of the regular habitation of the White Sea harp seal covers the Kara Strait zone, coastal waters of the northern one-third and probably also one-half of the western coast of Vaigach, southern extremity and entire western coast of Novaya Zemlya, and almost all the rest of the wide expanses of the Barents Sea except evidently its extreme southwestern pelagic portion falling under the warming influence of the Nordkapp branch of the Gulf Stream and bound by the actual position of the edges of drifting ice floes in the period of their maximum distribution. It is difficult to draw any precise boundary here.



287 Fig. 163. Range of the harp seal, *Phoca (Pagophilus) groenlandica* in the USSR (K.K. Chapskii).

The northern limits of the range in the Barents Sea cover the Franz Josef Land archipelago and roughly the same latitudes between it and Spitsbergen.

The Kara Sea does not wholly fall within the range: the extensive mainland expanses which, with some approximation, can be described by a wide arc from Vaigach roughly to Minin skerry fall outside the range. The harp seal is evidently not found southeast of this line. Thus it is wholly absent in Baidaratsk Bay, on the western coast of Yamal, in all the bays and straits fed by the waters of the Ob', Taz, Yenisey, Pyasina, and other rivers (Chapskii, 1938). The harp seal is extremely rare in the eastern mainland regions of this sea but is more common in the Novaya Zemlya strip from the Kara inlet right up to Cape Zhelaniya.

In the northeastern regions of the Kara Sea at 77 to 80° lat., the range extends in the form of a fairly long tongue from the line separating this sea from the Barents Sea, i.e., through a corridor between the northern extremity of Novaya Zemlya and Franz Josef Land. Much of the population entering here is evidently scattered in the western sections while a small proportion reaches Severnaya Zemlya. In very rare cases, under a favorable icy environment, extremely small stray groups are evidently capable of entering even into Vil'kitsk Strait.

The range of the harp seal in the White Sea is nowhere restricted and covers its entire area, including the bays. In the last century, seals often penetrated deep into Dvina Bay and were encountered even on Mud'yug Island (Danilevskii, 1862), i.e., almost up to the estuary of the Northern Dvina. They have been seen around those places and also on the Letnii coast, e.g., in Unsk Bay, even in this century. They transgress into Kandalakshsk Bay although they usually do not traverse far into its deep northern portion; however, under unfavorable conditions of the ice drifts stray young animals may be seen even in its extreme cul-de-sac sections. In Onezhsk Bay adults are not usually seen except for very rare transgressions into its northernmost section not far from the Solovetsk Islands; but young ones are seen there at times (rather rarely) (in the years of broken drifting "young" ice).⁹⁷ In Mezensk Bay this seal is quite common except perhaps for the extreme coastal waters along the southeastern fringe.

A feature of the range of the harp seal is its sharply manifest dynamic character caused by the migratory nature of the animal. These seals are not encountered simultaneously throughout the entire expanse of the range. They cover parts of the range in a certain sequence of regular

⁹⁷ The "invasion" of molted juveniles in 1966 following drifting "young" ice pools in a reverse direction against the general flow, was an unusual event (see page 425).

seasonal migration of the entire population or its individual age and sex groups. From late autumn throughout winter and in early spring all the harp seals are concentrated at the inlet to the White Sea and in the adjoining sections of the Barents Sea, from western Murman to the Pechora Sea. The range undergoes maximum constriction in the winter-spring period when almost all the White Sea population is concentrated in the White Sea and in the very near border sections of the Barents Sea. In this period the range evidently forms a ring of broad ice floe fringes whose rough position can be schematically depicted in the form of an uneven arc, with one end resting on the eastern Murman coast somewhere in the region of Cape St. Nos (and from there extends in a narrow fringe along the Murman coast even farther west and, in some years, up to the Norwegian coastal waters). The other end of the arc runs northeast beyond Kanin Nos toward the northern coasts of Kolguev Island and farther in the direction of Novaya Zemlya somewhat taking advantage of the edges of the ice floe belt. In a prolonged autumn and late winter, this expanse is more enlarged and extends farther northeast toward the Kara inlet. Such was the situation particularly in the first half of the winter of 1966-67, when the seals were confined in isolated herds throughout such a long broken edge (Beloborodov, 1969).

From autumn and very early in winter, the seals are often seen close to the coasts but there is not much information about their encounters due to the darkness and cessation of navigation. The animals remain exclusively in the water and tracing out their distribution even in the White Sea is quite difficult. Only from the beginning of February, when the period of reproduction is quite close and ice rookeries begin to form, is it possible to establish the location of the breeding section of the population. However, even right at the peak of whelping and lactation, when the female population with offspring is localized in certain parts of the White Sea, the location is not clearly known of the immature portion of the population and of those adults which, for some reason, have not participated in reproduction in a given season.

In April and up to early May, almost all the White Sea population is even more localized, mainly at the inlet and in the adjoining regions of Mezensk Bay, but quite often in the neck and even in the central basin of the White Sea, and partly right in the nearest regions of the Barents Sea, in the zones of the ice fringe. From mid-May the seals usually desert the White Sea, move rightward on the fringes in the most proximate region of the southern part of the Barents Sea, into the region of Kanin and Kolguev, and farther toward Gusin Land (Novaya Zemlya); later they even scatter on the new ice fringes of the Barents Sea right up to the Medvezhii and Spitsbergen islands, moving from the fringe increasingly

north and northeastward. At the end of July and in August, they reach the northern limits of the Barents Sea, transgress into the Franz Josef Land archipelago, in the northwestern regions of the Kara Sea, totally disappearing at this time not only from the White Sea, but also from the immense expanse of the Barents Sea.

In the high latitudes, along the edges of the arctic packs to the east of Spitsbergen and among the sparse drifting ice north and east of the northern extremity of Novaya Zemlya, the White Sea harp seal is quite scattered in small groups (sometimes adult males even singly⁹⁸) right up to early September, and later extends southward into the wintering ground. It is again concentrated at the time of reproduction in the White Sea region and the southeastern parts of the Barents Sea and small numbers are even seen in Cheshsk Bay.

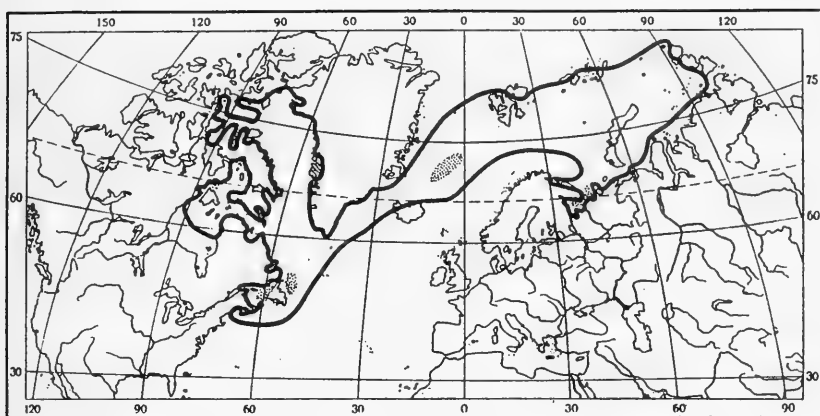
This, then, is a general outline of the seasonal dynamics of the range of the easternmost White Sea populations of the harp seal.

Geographic Range outside the USSR (Fig. 164)

Extends from the central and peripheral regions of the Barents Sea in a broad strip through the entire northern half of the Norwegian Sea and Spitsbergen Strait, northeastern and southwestern regions of the Greenland Sea (to the west and northwest of the Martovsk ice fringe) into Denmark Strait. The range encompasses the coastal waters of northern Iceland and encircles the eastern and western coast of southern Greenland in a relatively narrow strip. To the west of the meridian passing through Cape Farewell, the range includes Davis Strait and Baffin Bay (including the whole coastal periphery on the Greenland side as also on the western Canadian fringes). The seals are encountered in small numbers in Kane Basin and are more abundant in Jones Sound and traverse along Lancaster Sound up to the Wellington, Barrow, and the northern part of Peele straits inclusive. Depending on ice conditions, advance populations enter the Gulf of Boothia through Prince Regent Strait. The seals are common along the entire eastern coast of Baffin Island, the Labrador coast, in Hudson Strait, and in the northern part of Hudson Bay, descending along it almost up to the Belcher Islands. The southernmost part of the range encompasses all the sides of Newfoundland including the Gulf of St. Lawrence, the shelf along Nova Scotia, and probably the region of the Great Newfoundland coast.

The branch of the range diverging from the White Sea basin into the northwest along Murman extends rather irregularly around the Varanger

⁹⁸ Observations in the Kara Sea, southeast of the Blagopoluchiya Strait (K.K. Chapskii).



290 Fig. 164. Species range of the harp seal, *Phoca (Pagophilus) groenlandica*, and the site of its concentration during whelping and molt (dotted spots) (K.K. Chapskii).

Peninsula and the more western highly rugged Finmark coasts, descending to the Vesterälen Islands and even to the southern Lofoten Islands sporadically and only in cold winters and in spring. In extremely severe winters, as in the very early years of this century (especially the winter of 1902-1903), the herd of "invading" seals spread out even farther. Somewhat similar but much smaller "invasions" were observed on the Norwegian coasts even later.

The presence of stray specimens far beyond the limits of the normal range in the seas of Western Europe is extremely rare, episodic, at times even totally improbable. Such was the case of a gestating animal found floating in the Elba River 500 km upward from the estuary in 1896. Stray animals were sighted time and again on the coasts of Great Britain, from Scotland to the Thames. Stray animals were found on the northern coast of France. There is no reliable information about the sighting of these seals on the coasts of Sweden. In Norway the transgression of a stray juvenile into the extreme south was reported at Oslo Fjord in 1936.⁹⁹ (K.Ch.)

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Geographic Variation

The intraspecific structure of the harp seal was discussed even forty years ago. It has long been known that the entire population of this species is divided into at least three geographically isolated populations (or herds),

⁹⁹ Data on the episodic transgressions of seals were taken from Collett (1911-1912) and Moore (1952*).

each of which has its own features, extremely restricted areas of reproduction, and different regions of wintering and molt. Based on this, it was quite natural to decipher some morphological features characteristic of each of these populations. Even the earliest attempts to identify specific features of craniological indices (N. Smirnov, 1924, 1927, 1929) recorded some differences in average values between the different populations. These differences were subsequently refined.

Only one subspecies is known within the USSR.

White Sea harp seal, or "Lysun," *Phoca (P.) groenlandica oceanica* Lepechin (1778).

This is the largest form of the species.

The body length measured along the dorsal surface (L_c), according to the accurate data of Khuzin (1963), for males (100) is 169-204 cm ($\bar{x} = 185$), for females (300) 163-229 cm ($\bar{x} = 183$). The skull dimensions (according to the same source) are: condylobasal length in males (37) 200-234 mm ($\bar{x} = 217$), in females (300) 200.5-223 mm ($\bar{x} = 209.5$); mastoid width in males (37) 113-127 mm ($\bar{x} = 121$), in females (27) 111-124.5 mm ($\bar{x} = 117$); rostral width (at level of canines) in males (38) 32-46 mm ($\bar{x} = 36.2$), in females (27) 27.5-37.0 mm ($\bar{x} = 31.5$).

White Sea, waters of the USSR in the Barents Sea, and Kara Sea. The White Sea represents the zone of breeding.

Outside the USSR, this species is found in the waters of northern Norway and Spitsbergen and western and northern parts of the Barents Sea.

* * *

Outside the USSR, usually only one subspecies is recognized, i.e., the Newfoundland harp seal, *Phoca (P.) g. groenlandica* Erxl., 1777; during reproduction and molt, these are concentrated in two sections of the range: slightly northeast of Newfoundland Island and in the Gulf of St. Lawrence.

According to the accurate data of Khuzin (1963), the body length of males (83) is 152-195 cm ($\bar{x} = 176.5$), of females (127) 156-201 cm ($\bar{x} = 175.5$); condylobasal length in males (39) 200.0-219.5 mm ($\bar{x} = 208.5$), in females (41) 191.0-219.0 mm ($\bar{x} = 204.5$); mastoid width in males (40) 109.0-124.0 mm ($\bar{x} = 117.5$), in females (41) 109.0-123.5 mm ($\bar{x} = 116.0$ mm); rostral width in males (40) 30.0-40.5 mm ($\bar{x} = 33.5$), in females (41) 27.0-36.0 mm ($\bar{x} = 31.5$).

Statistically, the most reliable differences between the White Sea and Newfoundland populations are seen in the overall body length ($t = 8.52$) and in the length of the palate ($t = 4.61$) as well as in the condylobasal length and mastoid width of the skull, etc.

The range includes the northwestern, predominantly subarctic and arctic Atlantic including Davis Strait, Baffin and Hudson bays, and regions of the southwestern and perhaps southeastern coastal waters of Greenland.

The real subspecific differences between the Newfoundland and eastern Atlantic populations are also confirmed by the presence of a characteristic genotype in each of these groups (Naevdal, 1965).

Insofar as the Jan Mayen (Greenland) population, which is spatially well isolated, is concerned, it reproduces in the region of Jan Mayen Island and is generally distributed in Denmark Strait and the Greenland Sea; it reveals almost no statistically reliable craniological differences from the White Sea subspecies (Khuzin, 1963; Yablokov and Sergeant, 1963) and does not differ from the latter biochemically in the protein polymorphism (Meller, Naevdal and Valen, 1966*).¹⁰⁰

Thus this population evidently cannot yet be regarded as an independent subspecies; it represents a variety, tribe, or herd closely related to the White Sea harp seal; in fact, the two were regarded in the past as essentially similar (N. Smirnov, 1929). (K.Ch.)

Biology

Population. Although the total world population of the harp seal has decreased very significantly over the long period of its hunting, it was still regarded as considerable in the mid-1950s. It was approximately, but evidently overestimated, put at 5.5 million (Dorofeev, 1956) or 4.5-7 million (Scheffer, 1958). Out of the former assessment, 3 to 4.5 million were regarded as the Canadian-Newfoundland herd. This was followed by the White Sea population at 1-1.5 million. The Jan Mayen population at 0.5-1 million came third. A total figure of 3-3.5 million is evidently closer to the real position (Chapskii, 1966).

The harp seal is one of the few species for which the population has been determined by different methods, including aerial photographic survey. The latter procedure was used for the first time in the world in 1927 to count our White Sea herd. Part of the concentrated molting rookery was photographed, its area determined, and by extrapolation and assumption the population put at one million (Dorofeev and Freiman, 1928). This operation was repeated in 1928 and the total population of the White Sea herd was placed at 3-3.5 million (Dorofeev, 1939).

¹⁰⁰ At the same time, some other morphological features of the rank of the population were also identified; differences in body length, in distance between teats, and in number of asternal ribs and whiskers (Yablokov, 1963).

In the second half of the 1930s, new population counts were made based on different methodological procedures, i.e., by counting the mother seals (or the pups). The main stock (N. Smirnov, 1928)¹⁰¹ was initially put at 600,000-700,000 (P.A. Rudakov and N.V. Provorov). Somewhat later, double this figure or 1,300,000 was cited (N.V. Provorov).

The first postwar experiment in studying the White Sea population enabled a rough evaluation of this herd in 1947 at 1,200,000 (K.K. Chapskii).¹⁰² A quarter of a century after the above surveys and calculations, the same aerial photographic survey was again employed, which gave a figure of 1.2-1.5 million (Surkov, 1957). These figures incontrovertibly confirmed the sharp (by more than one-half) reduction in the population compared with the situation prevailing some 30 years ago. On the basis of this figure, however, no conclusion was drawn "about the adverse effect on the status of the reserves" by excessive hunting (Surkov and Khuzin, 1959)¹⁰³ and the herd continued to degrade for some time thereafter. In the 1960s, extremely disturbing warnings about its distinctly unfavorable position appeared in the press (Nazarenko and Yablokov, 1962; Yablokov, 1962; Yakovenko and Nazarenko, 1962; Yakovenko, Nazarenko, and Timoshenko, 1963; Yakovenko, 1963, 1967, etc.). The total population of the herd in the early mid-1960s was put at different levels: 400,000-700,000 (Nazarenko and Yablokov, 1962), 750,000
293 (Yablokov, 1962), a minimum of 400,000 (Chapskii, 1966), and a minimum of 225,000 (Yakovenko, 1963). The last figure is regarded as an underestimation (Khuzin, 1972*) although the mother population based on the data of a 1963 aerial photographic survey of rookeries was put at only 65,000. The total population in all the photographed molting rookeries in 1962 and 1963 did not amount even to 200,000. The total of the White Sea herd calculated on this basis did not exceed 300,000 by 1963 (Yakovenko, 1967).

The reduction in total population of the White Sea harp seal in the 1950s is also strikingly demonstrated by the dynamics of the shrinking areas of its nurseries and molting rookeries (Table 15).

The age-related composition of the productive population (Dorofeev, 1939) also served as an index of the adverse status of the productive proportion of the herd in which animals older than 10 years became very few in the early 1960s (Khuzin and Potelov, 1963; Khuzin,

¹⁰¹ That is, without pups.

¹⁰² Data for the 1930s-1940s have been taken from Khuzin (1972*).

¹⁰³ Assuming that all the 100,000 animals killed were pups.

293 **Table 15. Variation in the area of concentration (rookeries) of harp seals in the White Sea, km² (Yakovenko, 1967)**

Type of rookery	Year of observation							
	1953	1954	1955	1956	1957	1958	1959	1960
Rookeries in the lactation period (nurseries)	294	290	200	167	143	126	130	120
Rookeries in the molting period (molting)	85	75	64	58	58	48	46	48

293 **Table 16. Total average annual kill of the harp seal in the White Sea and in adjoining areas of the Barents Sea at five-year intervals from 1947-1964 (in thousands)**

1947-1951	1952-1956	1957-1961	1962-1964
190.0	125.2	117.6	89.7

1964). Hunting statistics too provided an equally striking account of the population reduction (Table 16).

As a result, an agreement was reached with Norway in 1965 to sharply reduce and modify the trend of marine hunting in this region. The measures adopted have already begun to show positive results.

A similar process of population reduction of the harp seal was also reported in the western fringe of its range where the Canadian population concentrates in the period of reproduction and molt. According to the calculations based on aerial photographic surveys in 1950 and 1951 of the nurseries in the Gulf of St. Lawrence and in the open Atlantic northwest of Newfoundland Island, the total reserves of these herds were put at roughly 3.3 million at the beginning of the second half of this century; of this, some 650,000 were regarded as pups (Fisher, 1952, 1955; Sergeant, 1959). Survey-based calculations gave somewhat lower figures for 1959 and 1960: the total population of pups in both the Newfoundland regions (in the gulf and in the "front" region) was put at 365,000. The basic stock (i.e., without pups) of both these herds was, however, put at only 1.2 million (Sergeant, 1963, 1965). The 1964 census confirmed these figures (350,000 pups) (Sergeant, 1965).

No census has been done of the Jan Mayen population but it has been roughly put at a maximum of a million (Fisher, 1954; Scheffer, 1958; Dorofeev, 1965; and others).

294 With such a dynamic nature of the range of the harp seal, its local population year round is also highly variable. By changing location from season to season, the population gathers sometimes almost wholly in relatively small sections of the range and at other times is scattered over a wide expanse (see above).

Habitat. The harp seal is a distinct inhabitant of cold waters but avoids the arctic pack ice, preferring the marginal zones and regions of stable drifting ice floes prevailing year round (as near Jan Mayen Island) or during low and high tides (as in the neck or inlet zones of the White Sea). It is this type of biotopic conditions that is selected by this seal in the periods of breeding and molt. In the course of these biological cycles, its herds appear deep in the ice massifs quite far from the marginal zones. In the breeding period it selects large stable ice floes and ice fields even with hummocks as a solid substratum. It is less choosy in the molting period and is seen on the fringes of large ice fields as also on groups of small ice floes if they provide a good link with the water body. This seal does not use the stationary shore ice (fast ice), as far as is known, under any circumstances.

Like the other pagophilic seals, the harp seal also crawls onto the ice floe but resorts to this mainly when the open water pools between the drifting ice floes on which it whelps are frozen.

At the end of the winter-spring period of reproduction and molt, the seals move to the fringes of drifting ice floes (at the beginning of summer) or are confined generally among the fairly sparse ice floes (in summer). At the same time, it is not quite correct to stress that the "harp seal spends its life among the ice floes round the year" (Freiman, 1939). At the end of summer, in autumn, and even in early winter, when these seals begin and continue to migrate southward and even appear in the region of breeding, the environment is no longer icebound (Chapskii, 1961).

Pelagic life is highly characteristic of the White Sea harp seal but nevertheless during the autumn migrations and on Murman even in spring, it is quite often seen around the coasts, transgresses into the bays, even those penetrating deep inland, such as the Kola, and may traverse through narrow straits, at times extremely narrow, such as the Zheleznye Inlet (on Loginov Island south of Novaya Zemlya). In the ice-free period, however, the seals distinctly exhibit a preference for the coastal strip and do not stray far from the coasts.

Food. The food of the harp seal, including our herd, in spite of the earlier optimistic assessment (Ognev, 1935) has not been adequately studied to date; the list of food objects is far from complete for much of the annual cycle, especially from June through January and February, when its feeding is very intense.

Among the invertebrates found in its food are the crustaceans, mainly euphausiids (genus *Thysanoessa*) and amphipods (genera *Anonyx*, *Gammarus*, *Themisto*, *Gammarocanthys*, and others), and also shrimps (*Crangon* sp., *Sclerocrangon boreas*, *Pandalus* sp., etc.); among the

plankton, mollusks of the genera *Clio* and *Limacina*. There is no accurate list of the species of cephalopods consumed, but these are mainly squids as also cuttlefish. Among the fishes consumed are capelin, polar cod, navaga, cod, coalfish [pollack], herring, plaice (*Hippoglossus*), sea bass, and even goby. At the end of the last and the beginning of the present century, harp seals fed along the Murman coasts quite regularly in spring as well as in autumn. This was the period of considerable increase in ice coverage of the Barents Sea and hence of a sharply reduced ice-free expanse, which constituted a seasonal contraction of effective area for the White Sea population of this seal. Fish was evidently the mainstay here, as confirmed by actual observations.

295 Earlier investigators may have erred in assuming that the harp seal consumed a sizable quantity of cod and even chased this fish away from the Murman coast (Knipovich, 1895; Knipovich, Yagodovskii, and Zhikharev, 1902; partly N. Smirnov, 1903; Breitfus, 1903) and also evidently in other regions (Allen, 1880; Wolleback, 1907; and others). Direct observations and dissection of the animals contradict these views. In the spring of 1900, from early March through the 20s of April, along the Murman coast, especially in the region of Kil'din Island, seals fed intensively on capelin (*Mallotus villosus*) and the stomach of 34 of 58 dissected animals contained fairly significant quantities of this fish (Breitfus, 1903). From the end of November, throughout December, 1902, and also in January and February, 1903, herds of seals wandered in the coastal waters of the western Murman and "their stomachs were stuffed with herring" (Breitfus, 1906). From the last 10 days of February through April end, 1905, the arrival of groups of harp seals on the Murman coasts was associated with the abundance of small coalfish (Prigorovskii and Breitfus, 1912).

Commencing from the end of lactation and molt, the juveniles seek food independently, feeding initially on large components of zooplankton present right among the ice floes. At the end of March the molted pups almost cease to look for small crustaceans and prefer to rest on the ice floes, resuming an active search for food in April. In this month their stomach or intestines mainly contained remnants of euphausiids (*Thysanoessa inermis* and *Th. raschii*) and amphipods (*Anonyx nugax*, *Parathemisto* sp., etc.) (N. Smirnov, 1903, 1927; Dorofeev, 1936; Sivertsen, 1941; Chapskii, 1961, 1964; and others). It is possible that the list includes the pteropod mollusk (sea butterfly) in the more northern regions.

Data are inadequate on the subsequent diet changes of pups on emerging (or drifting) into the fringes of the Barents Sea and also on the food of the adults there. At the very beginning of the 1920s, when the ice conditions along the Murman and northern Norwegian coasts

were unusual, the pattern of gradual intensification of feeding of the underyearlings and the enlarged species range of food items used by them were as follows. Initially feeding on minute plankton, the pups "later take to fish, at first polar cod . . . available abundantly among the ice floes . . . and later take to the food generally characteristic of this species, leaving no fish that is readily available, be it capelin or cod, surfacing from the bottom after it, and herring, and others" (N.A. Smirnov, 1903). There is some exaggeration here too about the cod. Smirnov also stated that "if herring were plentiful in the Murman, the bulk of 'skin' (i.e., harp seal, K.Ch.), mainly the young ones, would remain there" (N. Smirnov, 1903). Later, however, the views on this subject were more reserved and mainly "small pelagic fish or those confined close to the ice fringes" were added to the list of fishes consumed by the White Sea harp seal (N. Smirnov, 1924, 1927, 1935).¹⁰⁴

According to some investigators (N. Smirnov, 1903; Ognev, 1935), there are no differences in the nature of feeding between underyearlings and yearlings; according to others, however (Sivertsen, 1941), some differences do exist. Fish and deep-water and benthic invertebrates occupy a prominent position in the food of yearlings in addition to the pelagic crustaceans on which 1.5-month-old pups feed. Thus, the stomach and intestines of some yearlings caught in the White Sea in the last 10 days of April, 1934, sometimes contained in addition to the euphausiid, much larger crustaceans (*Crangon crangon* and *Spirontocaris turgida*) and amphipods, capelin being found more often (Sivertsen, 1941). Regardless of the foregoing situation, there is evidently no significant difference in the food of yearlings and adults.

- 296 The seals do not feed regularly during reproduction and molt, at least not daily; many generally remain hungry. Their stomach is often empty and highly shrunk. Of the hundreds of adult animals dissected at hunting sites in the 1920s and 1930s (Sivertsen, 1961), food was found in the stomach of two: March 15, 1929—male (the stomach was filled with euphausiids) and April 3, 1931—female (the stomach contained shrimps). A similar picture was observed in special investigations conducted at the beginning of the 1960s in the White, Barents and also Greenland seas. Not even one of the hundreds of animals examined contained food remains in the stomach. In most cases the stomach was markedly shrunk but its wall was very thick. In this period of such physical starvation the gastric juices were neutral (Shepeleva, 1963). According to other reports, the lactating females satiate themselves from time to time "if some food

¹⁰⁴ The "invasion" in Murman waters of this seal and the disappearance of cod there is a consequence of sharp atmospheric cooling (Linko, 1912; and others).

is available in the nursing region". The food comprises mainly planktonic or nectonic crustaceans (Surkov, 1960).

The seals not engaged in lactation or reproduction and living in this season in the more northern regions of the White Sea, along the fringes in the adjoining sections of the Barents Sea, and on the open Murman coasts, evidently feed regularly. Feeding is interrupted only in the period of molt when the animals mainly rest on the ice floes. In the years of deep penetration of these seals westward, into the Norwegian Sea, some instances are known of their being trapped in fishing nets set at a depth of about 200 m. Two animals were trapped even in the Arctic Circle, one of them in the region of Vardo even at a depth of 280 m (Collett, 1911-1912). With inadequate information on the behavior of such deep submergence, Nansen (1924, 1939) himself pointed out that, apart from the common fish food, the White Sea harp seal was capable of surviving on sea bass and flounder as well as on cuttlefish. Thus the "food spectrum" of the White Sea harp seal is evidently quite broad and has not been adequately studied.

In the 1920s, when the nurseries were located more northward, on the threshold of the Barents Sea, it was affirmed that the females at the end of the breeding season migrated for sometime, especially for feeding, to the Murman coast (Skvortsov, 1927; Dorofeev and Freiman, 1928). It is possible that such local migrations did in fact occur since the "young" ice floes at the time of the cessation of lactation often drifted away toward the Barents Sea. At the same time, such an interpretation of the movements of mother animals can be the result of inadequate reliable data. Regardless, such massive migrations have not been recorded in the past 40 years. In a much earlier period, as already pointed out, not only the adult females, but also other groups of the White Sea population were generally encountered feeding in considerable numbers on the Murman coast commencing from late autumn through the end of spring. Harp seals in particular were noticed here right from early March through the last 10 days of April, i.e., in the period covered by the formation of nurseries and molting rookeries. Evidently, the severe weather conditions in winter, as for example in 1901-1902 and some other years, exerted an unusual influence; in such years the edges of ice floes extended almost up to Kil'din Island.

The period of intense feeding now commences evidently from May, immediately after the cycle of reproduction, after which the seals desert the White Sea to molt. Breaking up into small groups along the entire edge and among thin ice floes, they feed mainly on macroplankton (the more massive species of crustaceans) and the polar cod scattered over immense expanses of the arctic seas. The summer-autumn range of the

harp seal is mainly dependent on the regions of distribution of this fish, which has great food value for the seal. Feeding in the high latitudes continues all through summer. With the onset of autumn, when the polar cod begins to form large schools and moves toward the coastal
 297 regions for spawning, harp seals pursue it. This fish is now almost the mainstay of these seals on the coasts of Novaya Zemlya, Kolguev, and Kanin, and especially in the northern regions of the White Sea. In the latter region, apart from polar cod, herring and partly perhaps navaga, represent important food items. Feeding in the autumn-winter period is no less intensive than in summer: everywhere in the coastal waters of the Soviet arctic, concentrations of seals and en masse arrivals of polar cod are noticed simultaneously (Klyuche,* 1936; Manteifel', 1943; Chapskii, 1938, 1961; and others).

Home range. The concept of home range is difficult to apply to the ecological features of this species whose populations not only migrate widely, but vary sharply in concentration in different seasons. The herd instinct in the harp seal is quite sharply manifest; it is evident even in summer when the population is highly dispersed, in small groups of usually not less than some 10 animals. One such "congregation" in which the animals are confined sometimes more closely and at other times less so (although usually not closer than 5 - 10 m) is separated from another by varying distances that are not conducive to numerical averaging. Evidently in regions of highly dispersed food objects (for example, the polar cod), the seals can be found in some cases even singly and far removed from each other.

During the autumn migrations, the animals gather into much closer and larger "congregations" but usually do not remain for long at one place. The age-sex structure of the feeding and migrating groups is not yet clearly understood; however, there is considerable justification for assuming that the migrants segregate into young and adults; the latter, even in high latitudes, then separate into sex groups, which is particularly noticeable among animals on the threshold of the winter-spring grounds. Here the concentration coefficient is also highly increased. The maximum density of animals in the White Sea occurs at the time of formation of the rookeries (Fig. 165). In 1963, mother seals were concentrated with their offspring at three sites over a total area of 108.3 km² where 60,000 whelped females were photographed (Yakovenko, 1967). In fact, the females there must have been somewhat more since not all of them were basking on the ice floes at the time of the aerial photographic survey. Assuming that some 10% of them had remained in water and making a correction of at least 5,000 accordingly, the average density of disposition of lactating females in the nurseries works out to roughly 600



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Fig. 165. Part of the harp seal rookery on ice floes in the White Sea. Photographed from an airplane (material of PINRO) [Polar Scientific Research Institute of Sea Fisheries and Oceanography, named after N.M. Knipovich].

animals per km^2 or one female in an area of roughly $1,660 \text{ m}^2$, i.e., at a distance of roughly 40 m from each other.

Actually, however, the mother seals are disposed far more densely and are not evenly dispersed, remaining in groups concentrated mainly along the fringes of large or finely broken ice floes that refreeze due to the formation of young ice floes at the site of open water pools or crevices. On these new ice floes extending in weird, twisted, and interlaced strips, tongues and much broader sections, the females and their pups gather in far denser groups than in the central parts of the ice

floes. Moreover, drifting ice floes with animals on them generally alternate with "vacant" ice floes (see p. 397). Thus the lactating females in fact live within some 5-10 m of, or even closer to each other.

In the molting rookeries the density is much higher: 165,000 animals of mixed composition (adult males, immature animals of either sex in the age of one year to five or six years, and adult females) covered a total area of 76 km² in 1963 (Yakovenko, 1967), i.e., average of 2,200 animals per km². In other words, there was one animal in an area of 455 m² (average distance of 20 m from each other). In fact, however, in this case too the molting animals are usually much closer, especially in the initial, exclusive male preserves where they literally rub shoulders, quite often in very dense rows almost fringing the edge of the ice floes (see Fig. 165). The sequence in the selection of biotopes is determined not only by the requirements under the definitive conditions of reproduction and migration, but also by the food factor, in particular the nature of the seasonal distribution of the polar cod, which is almost the mainstay of the White Sea harp seal and hence a factor responsible for the disposition of these seals.

Hideouts and shelters. A hard substratum (ice) is used by harp seals almost exclusively in the period of reproduction (for whelping, lactation, and partly mating) and molt, i.e., in the early spring (winter-spring) period. Very rarely, animals are encountered on ice floes even in the midsummer season in high latitudes (evidently the sick or well-satisfied animals induced by the excellent weather). Thus these seals reside in water for an incomparably long part of the year.

This seal never attempts to build hideouts in the snow on top of an ice floe, as done by the ringed or the Baikal seal. The only thing the White Sea harp seal is capable of doing is making air holes in the ice floe, a characteristic of most other species of pagophilic seals.

The mechanism of formation of the air holes evidently has no distinctive features. The seals resort to making them only in those cases when the open water pools between ice floes with pups on them begin to be covered by thick ice. The animals surfacing for respiration pierce the ice with their head. As long as they do not move to another site, they use the openings already formed, which are kept unfrozen by the animals through frequent surfacing and crawling out onto the ice. In the course of time these air holes assume the form of a low crater initially fringed by broken bits of ice and later by the water splashed during surfacing. Many animals can use the same air hole and hence there are usually fewer air holes in a nursery section compared to the number of lactating females. Since the ice floes in the breeding region are on the move constantly with open water pools usually occurring between them, the air holes do

not represent the lone means of contact for the animals between water and air.

The seals hardly use air holes in the much later spring molting rookeries, being accommodated by the natural openings in the ice floes in the form of open water pools, crevices, "gapes,"¹⁰⁵ and "partitions," which never close for long because of high and low tides, drifting ice floes, and floe movements caused by winds. In fact, there have been instances when the open water pools closed in high tide and froze when filled with ice bits. The seals surprised by hunters found themselves separated from the water. If, however, the "gape" is not densely or firmly frozen, the animals can put to advantage their weight and pierce the ice cover to hide below it. Similarly, the heavy animals can break up even thin young ice extending in quiet frosty weather over an open water pool or in cracks and crevices in the ice floes, especially by their combined might.

These seals resort to no other shelters. Only the newborn in the very first days of life on the ice floes seek some shelter from foul weather, creeping time and again into niches or crevices formed before they were born during the hummocking of the ice floes, or hiding under an ice floe overhang. Sometimes the pups hide so deeply under the ledges in piled up ice floes that they readily escape detection.

Daily activity and behaviour. The activity of the harp seal is not stereotypical from day to day; it differs in different seasons of the year depending on the characteristics of the successively changing biological cycles to which not all the age and sex groups of the population respond to the same extent. Thus there are periods of high and low activity. Animals participating in reproduction exhibit hyperactivity, which is somewhat more prolonged among females than males. For much of this period the males are even passive (up to the moment when their sexuality peaks, which is of relatively short duration). Females with pups, however, are active for at least 2-2.5 weeks of very intense lactation, though with intervals for whole days, since the pups are suckled not only during the day but at night, and go into the water many times between sucklings.

An extremely high motor activity, increasingly manifest in daylight, is noticed in the short mating period, accompanied by chasing competitors and seizures (see p. 400).

¹⁰⁵ Discontinuities formed between the frozen masses of ice floes, sometimes compressed (during compression) and sometimes diverging or enlarging (in low tide) are called "gapes" by the coastal hunters.

The last period, i.e., molt, is characterized on the contrary by maximum passivity, especially among males who rest in small groups on the ice for days on end without going into the water. The females, however, and also the young (commencing from yearlings) are still in the water at this time and join the males later. At the end of molt, the animals again enter a period of high motor activity and migrate into the zone of summer residence and intense feeding. Their "activity," directed toward procuring food in the zone of ice fringes in this period, can be assumed
300 to be manifested predominantly in daylight hours which rapidly increase. Nevertheless, their activity does not cease at night.

The summer behavior has not yet been clearly understood. Evidently, having expended considerable effort on migration into higher latitudes and feeding well on the way, the animals are now widely scattered in the northern limits of the range and do not exhibit much activity. The latter increases somewhat later with the commencement of reverse migrations, formation of herds, and transition to intensive feeding on fish in the autumn. Moving from place to place in autumn and early winter, on their way to the White Sea and in it, the seals avidly hunt for polar cod and other fishes during the day and also at night. Further, they are capable of submerging quite deeply, as demonstrated earlier by the example of some stray animals being trapped in fish nets set at considerable depths (see below).

The herd instinct is highly typical of the harp seal and is manifest not only in the formation of strictly localized rookeries in which almost the entire population of a region gathers. It is also reflected in all the behavioral features of these animals. The seals remain in herds everywhere, on the migratory courses, in the wintering sites, and in the feeding grounds. Only in the summer period is some deviation sometimes seen.

No aggressive tendency whatsoever is exhibited toward man under normal conditions; on the contrary, with the approach of man, the herd tends to leave the ice floe. However, the maternal instinct is so intense among the females that it suppresses the instinct for self-preservation and they bravely guard their pups without regard for themselves. There are no reports of any scuffle whatsoever among the animals except during the mating season.

Adults and immature animals are not heard but a hungry pup calls its mother with a loud wail, quite similar to the cry of a child.

It is difficult to establish with certainty which of the sense organs are better developed. Reports that these seals are "frightened" by ship smoke have no serious basis as the olfactory faculty is the least developed in all the pinnipeds. Their vision is quite good in water as well as

on land. Near, rather than distant, sight is probably better on land. The auditory faculty is evidently well developed. The ability to echolocate is beyond doubt among harp seals; otherwise, it is difficult to explain how this animal can orientate itself in water and catch quarry at depth even under conditions of the polar night. This faculty has been demonstrated experimentally by recording underwater sounds in a hydrophone (Mohl, 1968; L. Popov and Pleshakov, 1970).

Seasonal migrations and transgressions. In the nature of its migration, the harp seal has almost no peer in the family of true seals (Phocidae). Only the hooded seal and partly probably the Caspian seal are comparable, but the latter falls behind sharply in the magnitude of this phenomenon. Although this aspect of the ecology of the harp seal was known from the earliest published works, i.e., at least from the last quarter of the eighteenth century, it has not been thoroughly investigated so far and much is yet unknown.

In particular, all the details of the migrations of a well-fed juvenile which leaves the breeding site for the first time, are not known for certain. In fact, the initial migrations of the under-yearlings bear a passive character depending on the general drift of the ice floes on which the pup continues to rest for sometimes (up to March end to early April) after the final molt (i.e., transformed into a gray pup).

Under normal conditions of the White Sea basin with sharp drifts (i.e., when the ice floes drift northward through the neck into the inlet), the gray pups present partly on the ice floes and partly in the open water pools between them, drift in the same direction as the ice floes. Under the influence of this drifting, the pups ultimately find themselves in the northernmost regions of the White Sea or even beyond, on the fringes of ice floes in the southern sections of the Barents Sea. Here the gray pups feed from time to time and remain for sometime, possibly until they are overtaken by the molted adults, i.e., firstly the adult males and later the immature animals of both sexes, as well as gestating and wandering females. All this represents only a working model as accurately as the actual picture can be deciphered.

One cannot entirely agree that the gray pups abandon "young" ice floes for arctic latitudes solely guided by some subconscious desire to reach the north (Danilevskii, 1862). The situation that prevailed in 1966 demonstrated that such is not so. The exceptional complexity of the icy environment in that year, caused by steady northeastern stormy winds, disturbed the normal pattern of the ice drifts. The ice floes on which whelping occurred were not transported into the White Sea inlet nor into the Barents Sea, but were pressed to the western and southwestern coasts of the White Sea where they thawed with the onset of warmth. The

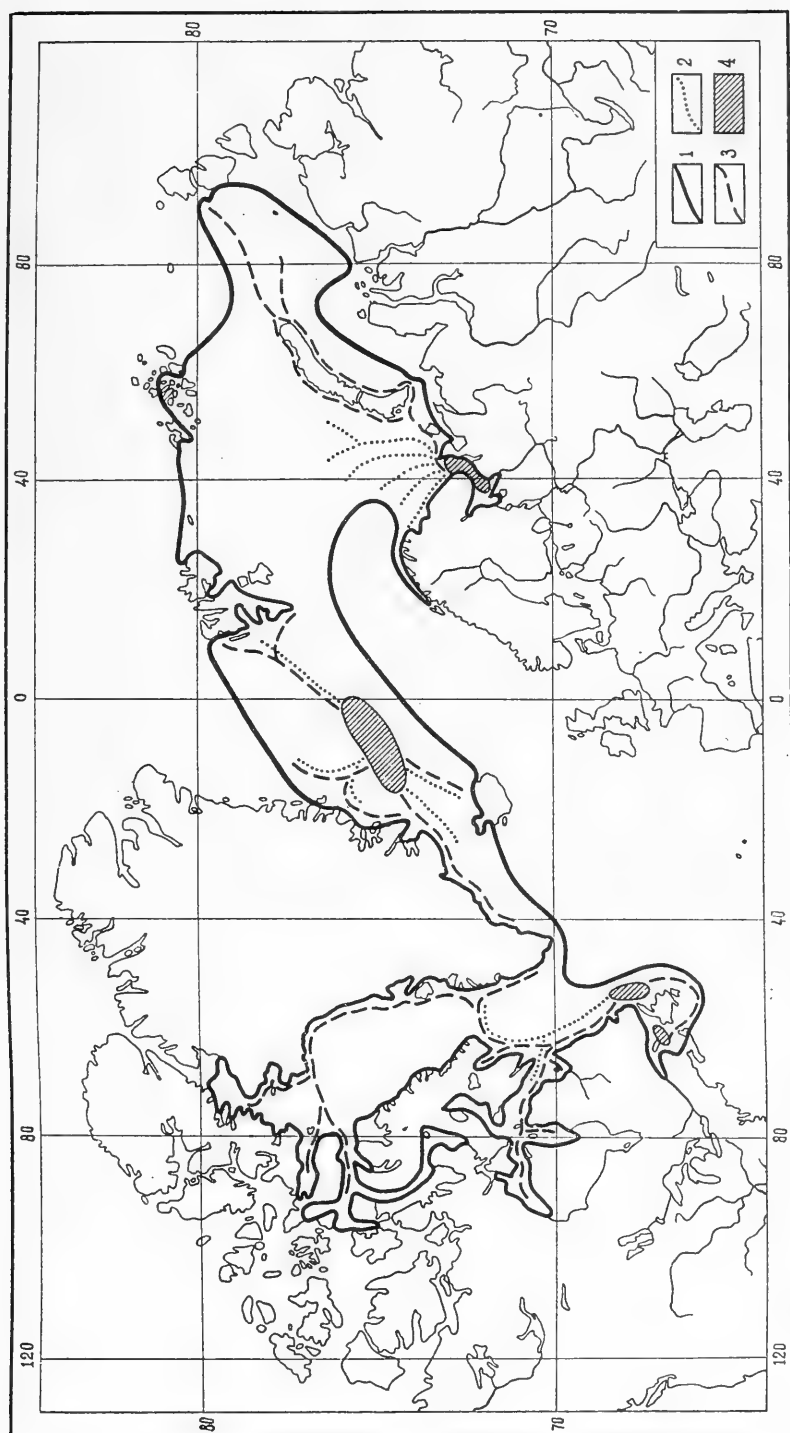
molted juveniles on these ice floes and in the water around them thus found themselves not in the northern sections of the White Sea, but on its western and southern fringes where they strayed in early summer into totally unexpected places, up to Arkhangel'sk and Kandalaksh inclusive.

By the end of April to early May, when the White Sea harp seal is quite prepared to emerge from the region of breeding but not yet wholly joined by the migrating stream, almost all the White Sea population is concentrated in the northern parts of the inlet zone, on the threshold of the Barents Sea, and in its southernmost sections. Here the seal population is partly confined to large rookeries and partly highly scattered in the form of small herds and groups on the ice floes as well as in the water. Their actual disposition, no doubt influenced in the recent past by hunting, depends mainly on the position of the ice fringes, on the characteristics of the ice regime, the nature of distribution of the ice floes, and on other as yet unidentified factors.

As soon as the majority of the seals complete molt and the molting rookeries in the White Sea are disbanded, the movement of the animals along the fringes of the ice floes of the Barents Sea becomes evidently somewhat more active. The herds spread increasingly along the fringes and, as they recede, move farther northward and ultimately reach the summer range.

The directions of spring migrations (Fig. 166) do not remain strictly constant but depend on the contour of the ice fringes. However, these migrations can be generalized schematically as follows. During May and June the movement of the seals from the southern parts of the Barents Sea proceeds initially along an arc approaching quite closely to Kanin Nos, Kolguev Island, and Gusin Land. Roughly on the latitude of the latter, in spite of the disposition of dense massive ice floes, the animals sometimes move north, sometimes to the northwest along the ice fringe receding gradually northward, and scatter almost up to Medvezhii Island and to the ice floes surrounding Spitsbergen. When, however, a rather large batch of the population thus moves west of the meridian of the Kola Peninsula, the ice floes even to the east of the Barents Sea rise markedly northward; they open up in July and by August provide access for the seals into the northeastern regions of the sea.

Following the receding ice floes and holding on mainly to their fringes, large numbers of the White Sea harp seal reach high latitudes in August, presumably spreading increasingly predominantly in the eastern regions of the summer range. However, on their northward journey in the spring-summer period, they often cannot reach the coasts of Novaya Zemlya directly which are still blocked by ice floes, although the seals are
 303 evidently numerous along the outer edges of this icy belt. In July-August,



302 Fig. 166. Figure showing the migrations of the White Sea harp seal, *Phoca (Pagophilus) groenlandica* (K.K. Chapskii):
1—boundaries of the range; 2—spring, and 3—autumn migrations; 4—regions of reproduction and molt.

a considerable number of them are seen in the broad corridor between Novaya Zemlya and Franz Josef Land. Some herds penetrate the straits of this archipelago while a much larger number of them transgress into the northwestern part of the Kara Sea. Small groups go east, sometimes very far, reaching the western coasts of Severnaya Zemlya.

Migration in the reverse direction commences in September. Now, abandoning the zone of the ice fringes, which in the autumn holds no special interest in the context of food availability, the seals go south and southwest (and in the western boundaries of the range possibly even southeast), and probably through the open sea. Unlike the spring migrations, on their reverse course, which has not been thoroughly studied, the seals determinedly adhere to the Novaya Zemlya coasts. One of the most important stimuli for their approach to land is the commencement of arrival of spawning polar cod along the coasts on which all the arctic seals feed in this period.

In the region of Cape Zhelaniya, harp seals are seen even in September and later at almost all the other points on the west coast right up to the southern extremity of this vast twin island. More often, they move from one cape to another and more rarely are seen in the deep bays and straits. The White Sea harp seals migrate southward in small numbers along the Kara Sea, i.e., the eastern side of Novaya Zemlya, emerging into the Barents Sea through the Kara Strait. Further advance to the White Sea has not been well traced but nevertheless it may be assumed that the migratory routes in the Pechora Sea run for the most part away from the mainland coast, which the herds of seals rarely approach and, that too, only on the western side of the Russkii bend. They probably do not transgress deep into the Cheshsk Bay; they are, however, more common on the northeastern coasts of the Kanin and partly Kolguev islands.

The seals arrive in the White Sea usually slightly earlier and begin to form their first nurseries there. In one or the other sections of it, predominantly on the right bank, these seals are encountered even from November end to early December, their appearance being also associated with the arrival of the polar cod. The autumn migrations, like the summer-spring ones, are mainly based on the food factor, especially the schools of spawning polar cod. It is therefore not wholly correct to interpret the autumn course of the harp seal to the White Sea as exclusively "migration for reproduction" (Freiman, 1939). This phenomenon is evidently more complex (Chapskii, 1961) since it begins to manifest at least 5.5 months before the forthcoming actual breeding season and the phenomenon covers even immature animals. This, if one may say so, complex stage of stereotyped behavior (countless generations have

well-worked out the course) in which the feeding seasons and the return of the animals to their original sites, guaranteeing the performance of the concluding stages of the annual cycle, has evolved with an accuracy that is perhaps maximal for biological systems.

In the past, in very cold years, when drifting ice floes in the Barents Sea came close to the western Murman and the White Sea harp seal rookeries were disposed in the inlet of the White Sea and the entire seal population in the spring period gathered in the inlet and in the comparatively small space extremely close to the Barents Sea bound by the fringes of drifting ice floes, the seals undertook extensive migrations along the Murman coast to the west. In particularly icy, cold springs, they moved not only up to Finmarken, but even to the coasts of northern Norway; turning round Nordkapp, they approached Lofoten and moved even more southward. Particularly memorable are the invasions of seals in 1901-1902 and 1902-1903 when the winters were unusually severe and ice floes were seen even in May close to the western Murman coasts and the southeastern fringes of the compact floating ice floes "lay" on the Murman coast considerably more westward of the White Sea inlet, almost around Kil'din Island. The large concentration of seals pressed by the ice floes at this time toward the Murman coasts caused the distant movement of some herds into Norwegian waters.

In the relatively less snowy years, however, when the waters on the coasts of the western Murman were not so intensely cooled and the winter-spring fringes of the ice floes remained far away in the north and east, transgressions of the seals along the Murman coasts were not so massive. Until the beginning of the 1930s, harp seals were quite common in the winter-spring months all along the Murman and were trapped there at many places in nets. Invariably, the herds initially came from the east, from the side of the White Sea and, after wandering, invariably returned again eastward. Their encounters continued usually throughout the winter-spring period, mainly in the spring, up to May, and sometimes even in June.

Now, in the 1960s and the 1970s, the nurseries are usually disposed deep in the White Sea while the spring boundary of the drifting ice floes in the Barents Sea runs far northward of the Murman. For this reason and also because of the sharp population reduction on the Murman coasts, harp seals are encountered comparatively rarely.

The Newfoundland group of seals begins to move northward from the regions of reproduction and molt even from the end of April. They move along the fringes of the ice floes blocking the Labrador coast toward Davis Strait and their courses branch somewhere at the latitude of 60° and along 60° W long. A relatively small portion of the population

continues, as far as the snowy environment permits, to move northward up to the southeastern region of Baffin Island. Another, much larger portion, as far as possible, moves through Hudson Strait into the north-western and eastern regions of Hudson Bay. A third group, representing the greater bulk of the migrants, deviates into the northeast and reaches Greenland roughly at the latitude of 65° or slightly more southward; later, the majority of them proceed northward and, depending on the situation of the ice floes, diverge radially along the straits of the Canadian archipelago, along the eastern coast of Baffin Island, and north into Kane Basin.

A small group of the population turns southward up to Cape Farewell and, probably running round it, reaches the eastern side of southern Greenland (Sergeant, 1963; Mansfield, 1963).

The reverse migrations, traced slightly better, proceed from Baffin Bay along two main routes: one runs along the coasts of Greenland up to its southern tip and from there traverses through the open sea toward the southern part of Labrador. Another group, gathering from the Canadian straits, runs along Baffin Island and taking the branch from Hudson Strait continues along the Labrador coast. Evidently, at the southern corner of the Labrador Peninsula, which the seals reach by November, both the routes converge and deviate again along the Strait of Belle Isle. Along one of them following the eastern banks of Newfoundland, the animals turn farther southward. It was formerly assumed (Robinson, 1897; Chafe, 1923; Nansen, 1927*, 1939) that the seals rushed toward the great fish banks in the southwest of Newfoundland. New information (Sergeant, 1963) does not, however, confirm this view. Another path proceeds through the Strait of Belle Isle into the Gulf of St. Lawrence. It is not clear where the seals of this herd remain from the middle of January to February end and which courses they take to gather in the nurseries.

Exact information is not available on the migrations of the Jan Mayen seals. At the end of the lactation period, the pups drift with the ice floes and later emerge onto the fringes; the rest of the animals wander in small herds to the northeast and southwest of the region of the rookeries. It is difficult to say whether the seals diverge simultaneously in opposite directions or these directions alternate in some manner.

305 Judging from tagged pups, in some years (for example, 1953), the animals are mainly carried away in one direction toward Denmark Strait; in other years (especially in 1955), mainly in the same direction, but also in the opposite direction (Rasmussen and Oritsland, 1964). The zone of summer-autumn dispersal of the Jan Mayen herd extends along the fringes of the ice floes blocking the eastern coasts of Greenland,

from Denmark Strait (and probably even from the southernmost part of Greenland) to Spitsbergen. In the latter region these seals probably meet with their White Sea kin and sometimes are drawn by them onto the icy rookeries in the White Sea. Transgressions of stray tagged animals from one region to another are known.

Reproduction. Although the harp seal forms no harems whatsoever like the other seals reproducing on ice floes, it should not evidently be regarded as strictly monogamous. This concept is in general not applicable to the White Sea harp seal. Even in the days preceding mating, no single male picks up a female for mating as happens in the case of the larga. In the same manner, and immediately after mating, the male does not stay with the female nor does he accompany her in the following days. The males and females converge only for coitus and the entire mating behavior of any given pair, including "heat" and contentions over a female among the suitors, lasts barely for a day.

Not long before the onset of the mating period, which becomes evident from the growing activity of the males, the latter gather near the whelped females in small but fairly close rookeries ("monasteries") as though in anticipation of mating. When the time comes, they are aroused from their torpor and these heavy and awkward animals exhibit surprising activity on the ice floe. They crawl along it, dive into the water one after the other, surface from the open water pools, noisily chase each other, as if in play exhibit surprising dexterity, and again dive into the water. In earlier years it was not always possible to perceive from afar in this melee, even with binoculars, who was chasing whom—whether the males were chasing the females or the suitors were chasing each other. As a result of organized scientific floating stations on ice floes, it has become possible to study the intimate life of the White Sea harp seals quite closely and quite completely.

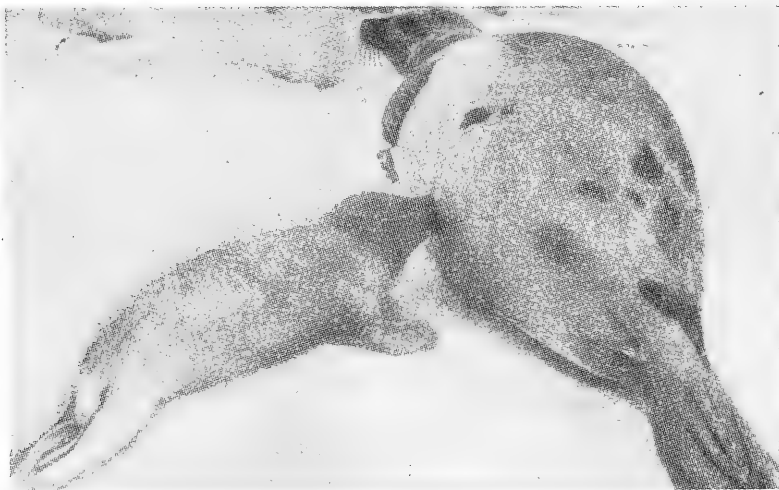
The period of mating is accompanied by powerful excitation of the productive males and rather serious scuffles occur among competitors which can even draw blood (R.Sh. Khuzin). Sometimes the competitors are severely injured with bleeding wounds. The victor remains alone with the chosen female far from the rest of the animals. Coitus proceeds in water (evidently more often) as well as ice floes.¹⁰⁶ In the latter case, it extends for 20-25 min (Yakovenko and Nazarenko, 1971*). It is highly possible that the scuffles taking place between productive males is a consequence of the acute competition among them arising from the

¹⁰⁶ There are some other views, although hardly substantiated, that the animals do not mate in water but only on ice floes (L. Popov, 1966).

quantitative disproportion between males and females due to long-time preferential killing of the latter.

The mating period among White Sea seals sets in at the beginning of the first week of March and terminates evidently around the 20th of the same month. Thus the total duration of the mating period is not long—about 1.5-2 weeks for most of the animals. However, there are various views on this subject: not more than 2 weeks (Surkov, 1957), 10-12 days (Rasmussen, 1957), about 2 or 2-3 weeks (Dorofeev, 1960; L. Popov, 1960), and 10-20 days (Freiman, 1939). The views of some about a late mating season (as against the average) from March end to mid-April (G. Nikol'skii, 1933) and more so that mating occurred
 306 after the cessation of molt (Sleptsev, 1949) are erroneous. Even in 1902, the first of the mating pairs on ice floes were noticed on March 10 (N. Smirnov, 1903).

Most of the whelped females mate even before suckling of the pups has ceased—roughly in the second half of the period of lactation, closer to its end. The earliest recorded date of mating is March 4 (Sivertsen, 1941). Rarely, the last of the winged males was observed hanging around suckling females in 1948 on March 20. Twenty years later, these dates were rendered more accurate by researchers on the floating research stations in the White Sea (Yu.I. Nazarenko, L.A. Popov, M.Ya. Yakovenko). The first pair in coitus was observed on March 10 and the last on March 24 (Yakovenko and Nazarenko, 1961). At the beginning of April the testes of the White Sea harp seals revealed no mature sperm (Surkov, 1957).



The conclusion of the mating period is marked by the quiescence of the males, cessation of scuffles among them, a distinct coolness toward the females, and their departure with the young ice floes. By this time (in the second half of March), the males begin to form different herds (rookeries) initially consisting exclusively of adult males. These very intimate and massive groups, extending for kilometers along the edges of the ice floes, along the open water pools and partitions, mark the commencement of a new cycle of life, i.e., the molting period.

The period between mating and whelping is about 11.5 months. In fact, however, embryogeny occurs with a fairly prolonged lag in the stage of the blastocyst. The growth of the embryo commences roughly 2.5-3 months later when implantation sets in. Excluding this duration, the actual development of the fetus extends for slightly over 8.5-9 months. Until June, no distinct signs of gestation are seen in the womb (Nansen, 1924, 1939; G. Nikol'skii, 1933; Sivertsen, 1941; Fisher, 1955).

Having attained maturity, the females usually undergo parturition every year although there are no accurate data on barrenness to date. The view was expressed before (N. Smirnov, 1903, 1927, 1935; Kulagin, 1929) that the females of the White Sea herd do not give birth to young ones every year. However, this view was based on incomplete data and 307 has not been adequately proved. A thorough analysis of the generative organs leads more to a contrary conclusion (G. Nikol'skii, 1933; Chapskii, 1963): most of the whelped females mate again in the same year. In any case, there is no large-scale barrenness among the White Sea females; it does not exceed 10-15% of the mother population in this herd.¹⁰⁷

The proportion of barren females among the Canadian population too is not high though it has been put at 10 to 16% (Sergeant, 1966) and even 20% (Fisher, 1952, 1955) for the population of the Gulf of St. Lawrence.

According to the morphological indices of age used at present, males as well as females retain the reproductive capacity for over 15 years after attaining sexual maturity. The oldest of the investigated females that had whelped in a season were aged 20 years while the productive males included even 25-year-olds (Fisher, 1952; Rasmussen, 1957; Sergeant, 1966; Yakovenko, 1967). Thus it may be assumed that males as well as females retain their reproductive capacity up to 25-30 years although under conditions of extremely intense hunting it is indeed a rare animal that attains this age (fraction of a percentage).

Unlike the other arctic seals, harp seals bring forth their offspring in strictly localized sections of the winter-spring range, which for the

¹⁰⁷ In calculating the population dynamics, the barren animals among the females were frequently not taken into consideration (Yakovenko, 1967).

species as a whole number four: (1) Gulf of St. Lawrence; (2) region to the north-northeast of Newfoundland Island close to the Strait of Belle Isles (seals of the Canadian population); (3) region of Jan Mayen Island; and (4) the White Sea. The ice regime characteristics in a given year or even a very prolonged period of this regime exert an influence on the actual location of the nurseries, which therefore vary from year to year within certain limits. These locations also change in the course of a given season under the influence of drifting ice floes.

Seals of the White Sea herd form nurseries depending on the conditions of the ice formation either in the neck or in the central basin (more often on the threshold of the neck and sometimes even in Dvina Bay) or in the inlet of the White Sea. The possibility in some rare years of a small proportion of mothers giving birth in Cheshsk Bay (Danilevskii, 1862; Zhitkov, 1904; Suvorov, 1913*; Vinogradov, 1949; Dorofeev, 1956) has not been confirmed and should be regarded as erroneous.

Over the last 30 years the formation centers of White Sea nurseries have undergone significant changes. In the 1920s, rookeries were seen almost exclusively in the inlet comparatively close to the fringes of the ice floes in the Barents Sea. From the mid-1930s (1935 - 1936), however, they began being formed considerably farther away, toward the southwest, i.e., in the neck and the central basin. The desire to provide for the juvenile adequate conditions in which it can grow well until it becomes self-supporting has compelled the females to select regions much before parturition with sufficiently large and stable ice floes capable of withstanding compression and hence able to serve as a reliable substratum for the pup's residence for many days. Another invariable condition for the formation of the nursery is the presence of a fairly dense network of open water pools, fissures, and gapes, which permits the female to approach the chosen ice floes while maintaining contact with the water (Fig. 165).

308 The sum total of these conditions together with the herding tendency (which to a large extent is probably caused by these factors) and also the sharply manifest seasonal migrations due to concentrations of the population in a restricted section of the range, necessitate that gestating females gather periodically in large numbers in the regions of reproduction. Immediately before whelping, they crawl onto the ice to form nurseries. A nursery may run into several tens of kilometers and the area several hundreds of square kilometers. Initially, there is only one nursery (rarely two or more) but over time, under the influence of drifts and shuffling of the ice floe, the single massive nursery is fragmented. As a result, at the end of lactation, when the suckling females leave the young ice floes, several individual groups of juveniles are seen in what

was once a large single nursery. Usually, by this time the juveniles are transported by ice drifts for long distances from the site of whelping.

Under the influence of the prevailing surface flow from the White Sea into the Barents, nurseries formed initially in the central basin or in the neck are gradually transported into the inlet where they cease to exist. There are, of course, exceptions to this rule. An example is the situation that prevailed in 1937 when ice floes with pups in the final stages of molt were transported far westward into Kandalakshsk Bay. The very same phenomenon, far more acutely, was repeated in 1966. This clarifies the view expressed by Acad. I. Lepekhin (1805) about some retreats in the spring migrations of the White Sea harp seal juveniles when they attempted the inner regions of the White Sea.

The animals are disposed unevenly in the nurseries. The gestating females usually select large ice floes and are disposed initially along their peripheries. In time, they often crawl toward the center of the ice fields and thus their distribution becomes more uniform. On the whole, however, within the nursery the animals occupy not all the ice floes but only some of them, usually those along the open water pools and fissures. Therefore, the rookery does not appear compact but has alternating occupied and vacant sections on the ice floes. Ice floes with seals densely or sparsely disposed on them alternating with "vacant" ice floes, cover an extensive area away from the coastal regions of the sea. The lesser the density of the rookery, the wider its area, and vice versa. Further, much depends here on the population of the animals, which is affected by the magnitude of hunting.

Shortened periods of whelping are a characteristic feature. Among the majority of White Sea mothers, parturition extends for not more than a week, from the last few days of February to the first few days of March. In 1968, by March 4, almost all the gestating females had undergone parturition. It is the rare female that gives birth earlier than this period (but nevertheless not before the 20th of February) or slightly later. A survey of the animals in the month of March revealed that of the total number of white pups (916), the newborn (aged less than a day) on March 5 were only 12, or 1.4%; on March 7, 0.8%; March 9 about 0.4%; and on March 12 about 0.3% (Khuzin, 1970). In fact, some very late dates of the appearance of newborns, for example March 18 and 31 and even mid-April (Sivertsen, 1941) have been recorded but such instances are totally sporadic.¹⁰⁸ Evidently, taking into consideration such anomalous instances, the total duration of the whelping period is sometimes put

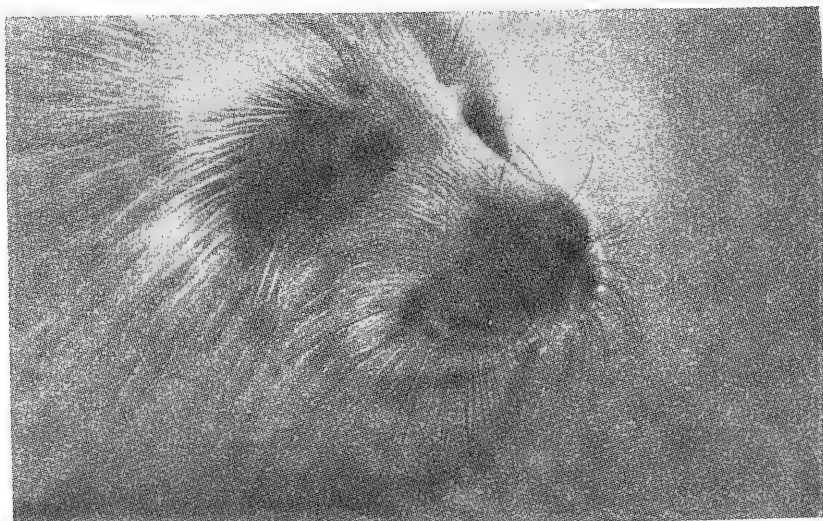
¹⁰⁸ In 1966, one white female pup with a firm hair coat was detected as late as April 26 (M.Ya. Yakovenko).

at about two months (Smirnov, 1935) and even extended to 2.5 months (Sivertsen, 1941). However, it is not correct to include in this period the extreme, absolutely atypical instances.

309 The exact moment of birth is usually beyond observation although one such instance has been described (Sivertsen, 1941). Some members of our hunting expeditions affirm unanimously that births occur very rapidly and, as a rule, with no particular birth pangs. Nevertheless, an instance is known of a dead, full-term pregnant female on the ice floes in the White Sea in 1959 (M.Ya. Yakovenko). Instances are more common of stillborn pups or those that perished soon after birth.

The birth of twins has not been established although, a century ago, it was stated that the females produce one pup, often two or possibly three, based on the fact that hunters sometimes found up to three pups on the stretch of an ice floe around a single female (Brown,¹⁰⁹ 1868). Similarly, rare instances of two pups cared for by a female equally well could point to such a possibility but only indirectly (M.Ya. Yakovenko).

Growth, development, and molt. The newborn is covered with a long dense, silky hair coat that is yellowish-white with a faint green tinge; hence a just-born pup is called a greenling by local hunters. Its length at birth averages 83 cm (in a straight line, *Lcv*) and along the dorsal surface



309 Fig. 168. White pup of the harp seal. White Sea (photograph by A.V. Yablokov).

¹⁰⁹ Significantly, however, this author pointed out that not a single hunter saw more than two fetuses in one womb.

(*Lc*) about 90 cm. The subcutaneous fat layer in a newborn is negligible or almost non-existent. The weight is generally about 7 to 8 kg.

In the first few days after whelping the females are particularly solicitous of their pups and remain with them almost constantly on the ice floes. The milk composition of the White Sea mothers, according to the latest data (Khuzin, 1970), reveals considerable variation: fat from 13.5-40.2% (average 29.35%), nitrogen 1.21-2.95% (average 1.76%), and protein content from 7.7-18.8% (average 11.17%) [see also Table 17]. Suckling is frequent, not only in the day but even at
 310 night. The suckling mother lies on her side and the pup alongside her stomach finds one or the other teat without difficulty. At times, even an approaching ship cannot coerce a suckling mother to abandon her pup. Sensing danger, she will crawl away attempting to carry the pup with her, then abandon it to dive into an open water pool or through an air hole in the ice but immediately emerge on the ice again. Having overcome her fright at the ship, she comes close to the pup and again dives only to reappear on the surface merely a few tens of seconds later. Confronted with imminent danger, she will not leave the pup out of her sight.

Even in the early period of its growth, the pup exhibits quite good mobility and traverses considerable distances, evidently not so much in search of its mother, as to find protection from wind, to which, lacking adequate fat reserves, it is initially very sensitive (Dorofeev, 1939). Perhaps, too, there is a natural need for movement. At favored sites, well protected from winds by an icy projection or the cornice of a hummock, the pups remain for long periods. Their prolonged resting at one place, due to the effect of body heat, forms a basket-like oval depression on the ice. Inside the depression the pup is always dry.

A few days after birth the green tinge of the pup's coat disappears and it turns white; hence hunters refer to it as a white pup. It gains weight rapidly and by early in the second week after birth has accumulated 9-11 kg of subcutaneous fat; its total body weight now goes up to 17-18 kg. The body length at the end of the white-pup stage averages 95-96 cm (*Lcv*) or 102-103 cm (*Lc*). The firm white hair coat is sported for roughly a week or one to three days longer (Sivertsen, 1941; Chapskii, 1964; M.Ya. Yakovenko, Yu.I. Nazarenko); the assumption of
 311 a long duration of this period, from 9 to 14 days (Dorofeev, 1936), is hardly correct.

The commencement of a perceptible loosening of the neonatal hair coat in the White Sea seal occurs roughly on March 8-9. Initially, the hair begins to weaken slightly, loses its original brightness and purity of color, and acquires a gray bloom. The gray bloom is often due to the thinning of the white hair coat (as a result of the pup's growth and



310 Fig. 169. Well-fed white pup of the harp seal. White Sea, early middle 10-day period of March, 1965 (photograph by A.V. Yablokov).

its dark skin showing through) and the growing new, already pigmented coat. Often the guard hair of the white coat turns gray at the base and the pigment penetrates there as long as the hair bulb is not atrophied (M.Ya. Yakovenko).

This state extends for a week, after which the next stage of molt sets in (Fig. 170). By this time the white cover has become even sparser and the growing stubs of new hairs can easily be seen through it. A few days later, molting becomes even more evident: the white hair that has turned gray falls out in large clumps almost simultaneously from the head, hind and fore flippers, exposing a darker, short, and rigid hair coat. Following this and almost simultaneously, rapidly growing bald patches on the back and tail appear. The last hair to molt is that of the ventral side and body flanks. The better fed the pup, the more rapid the molting of the white coat. In underfed pups, who have lost their mothers early, molting is not only impeded or even halted, but acquires a different sequence: the primary coat is retained on the flippers, tail, and head longer than on other parts of the body.

Lactation ceases in a normally molting pup at three weeks of age (Fig. 171). The normally fed molting pup at this time is, on average, 106-108 cm (L_{cv}) or 114-115 cm (L_c). Its total body weight averages 32-33 kg, and some even 38-40 kg or more; the subcutaneous fat with the skin (blubber) weighs 22-23 kg. The fully molted pup is called a



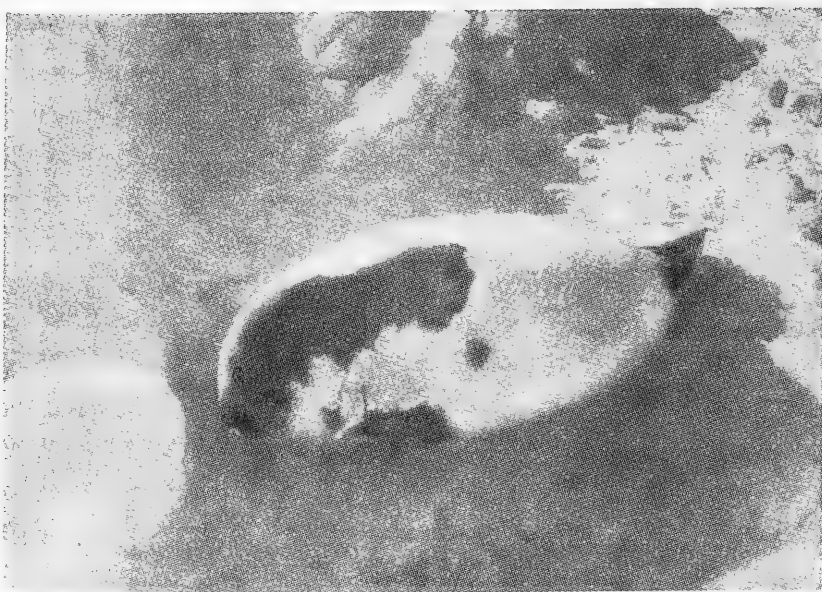
311 Fig. 170. Normally fed molting pup and a pygmy (sick pup of the harp seal).
White Sea (photograph by M.Ya. Yakovenko).

312 gray pup. The hair coat is extremely similar in color in yearlings and two- or three-year-olds but differs in greater density and softness; the older juveniles also differ in body proportions: relatively larger head and longer flippers. The main gray background of the skin among gray pups is darker on the dorsum with brown angular, predominantly small spots scattered here and there. On attaining roughly one month of age, the pup under normal conditions enters the water for the first time and commences an independent life.

The whelped females no longer spend as much time on the ice flow as necessitated before. Their residence outside water follows a definite pattern ordered by periodic lactation, depending on the time elapsed from the moment of parturition, and the weather factors.¹¹⁰ On pleasant, quiet, and sunny days, 85, 90, and even 94% of the total mother population can be seen on the ice surface in some sections of the rookery.¹¹¹ On the contrary, in stormy weather, this index drops to 36-45%

¹¹⁰ Detailed information on the periodicity of lactation and the general regime in nurseries was provided by the floating ice stations organized from the end of 1966 directly in the rookeries. Groups of investigators landed by helicopter on the White Sea ice with tents and the requisite equipment and carried out extremely interesting studies (L. Popov, 1966, 1967; Khuzin, 1970; Yakovenko, 1970; Yakovenko and Nazarenko, 1971*).

¹¹¹ According to others (L. Popov, 1966), however, on such fine days, 45-55% of the whelped females were seen on the ice during the day and up to 70-80% in the evening.



312 Fig. 171. Normally molting pup of the harp seal (photograph by M.Ya. Yakovenko).

and on March 7 even further, to 11% (Yakovenko and Nazarenko, 1971*; L. Popov, 1966).

Even in the early period of lactation, not all the whelped and lactating females are seen simultaneously in the nursery although they maintain a definite feeding cycle. The maximum number on the ice floe varies at different times: evening, midday, or morning hours, but
 313 more often peaks at midday and evening. The maximum percentage rarely approaches as high as 85-90%; it is usually lower, around 70%. It decreases in the course of time and the residence of the suckling mothers on the ice floe dwindles. In the first few days immediately after parturition, they remain on the ice floe for long periods and feed the pups most often at 3-3.5 hr intervals even during the night. At this time of lactation, the pup receives roughly 0.75 liter of milk in one feed. Later, as the pup grows, feeding becomes less frequent (4-5 times) and the pup then suckles a larger amount of milk per feed (about 1.2 liters). At this time the lactation schedule in most cases is as follows: (1) at 6:00-7:00 a.m., (2) 10:00-12:00 Noon, (3) 4:00-6:00 p.m., and (4) 9:00-11:00 p.m. Further, suckling continues even after midnight until the morning feed, as evidenced by the cries of pups and their quiescence after sometime, evidently after satiation of hunger (Yakovenko and Nazarenko, 1971*; Popov, 1966). The daily requirement for milk in

the first few days is about 4.5 liters, which later goes up to 5.8 liters (Yakovenko and Nazarenko, 1971*; Popov, 1966).

The milk of the harp seal contains 42-44.5% fat and 8.4-12% protein (Sivertsen, 1941; Dorofeev, 1960). Table 17 shows the composition of milk (10 samples) according to the more accurate data of Khuzin (1970).

With such a high level of well-being, the daily growth of the pup in a short period of time—from greenling to white pup beginning to molt intensely—averages 1.4-2.3 kg (Yakovenko and Nazarenko, 1971*).

Pups which have completed normal lactation and molt grow heavy and round like dumplings; they remain for one more week and sometimes longer on the ice floe until the white wool is completely shed and the gray coat begins to grow. During this period of starvation, extending for about one-and-a-half weeks, the normally fed pups lose, on average, about 5 kg of body weight, roughly averaging 0.5 kg (Chapskii, 1964) or 0.6-0.7 kg (Yakovenko and Nazarenko, 1971*) per day. Such a weight loss in no way affects the future well-being of the young one on its taking to independent living in water.

However, not all pups receive normal feeding; pups are encountered which have been abandoned early by the suckling mothers or have lost their mother for other reasons (Fig. 172). If at the age of one week, the fat deposition in the pup does not exceed 6-7 kg (and their total weight not over 10-13 kg or slightly more), cessation of lactation inevitably leads to emaciation and later to the pup's death.

The subsequent growth of the animals proceeds more slowly but continues not only in the first few years, but right up to the time of attaining sexual maturity though at a very slow tempo (Chapskii, 1952; Yakovenko, Nazarenko and Timoshenko, 1964*; Yakovenko and Nazarenko, 1967; Khuzin, 1967; and others).

314 Earlier there were no reliable morphological age criteria and the period of attaining sexual maturity was reported variously as: not before two years of age (Nansen, 1924, 1939), at three years (N.A. Smirnov, 1927), not before four years (Bartlett, 1927*; Nikol'skii, 1933), and even five years (Degerbol and Freuchen, 1935). At present, when the age of

313 Table 17. Composition of the milk of the harp seal, % (Khuzin, 1970)

Fat			Nitrogen			Protein			Ash		
Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean
13.53	39.24	29.35	1.21	2.95	1.76	7.73	18.81	11.17	0.51	1.47	0.82



314 Fig. 172. A typical underfed pup (dwarf) of the White Sea harp seal with remnants of embryonal (white) hair coat on the head and flippers. White Sea (photograph by M.Ya. Yakovenko).

a given animal can be accurately established within a year, the age at which reproduction commences has been well substantiated.

The period of maturity among the female harp seals extends for several years. In the White Sea population some females ovulate for the first time even at the age of three years, with the percentage of such early maturing females reported variously as 5-12 to 15.5 (Yakovenko and Nazarenko, 1967) or 30% (Chapskii, 1963). According to these same data, about 50% mature by the age of four years but slightly less (36%) according to other authors (Yu.K. Timoshenko). The rest of the females mature at five or even six years (Khuzin and Timoshenko, 1968*) but some, however, at seven years (Fisher, 1954; Rasmussen, 1957; Sergeant and Fisher, 1960; Sergeant, 1966; Yakovenko and Nazarenko, 1967; R.Sh. Khuzin). The average age of the onset of sexual maturity among the female White Sea population in the second half of the 1960s was established roughly at 4.5 years (R.Sh. Khuzin). Evidently, however, the average age of females that have attained maturity varies within certain limits, depending on the intensity of hunting, especially on the replenishment of the mother population by those of the younger generation that have escaped the hunters. It is significant that over the decade from 1953 through 1962, the average age of the Newfoundland females that had attained sexual maturity fell from 5.5 to four years (Sergeant,

1966). Males develop somewhat more slowly and their maturity sets in, in most cases, at five years of age (Chapskii, 1963). According to some other data (Yakovenko and Nazarenko, 1967), even four-year-olds are
 315 mature. On the other hand, Newfoundland males become capable of mating generally at seven to eight years of age (Fisher, 1954).

The uterus (without vagina) of the lactating females two months after parturition weighed about 200 g. The weight of the paired ovaries (their average) in such females varied markedly, from 6 to 10 g; the testes of adult males in the breeding season without the spermatic cord weighed 135-300 g and 200-370 g with it; their length varied from 10-14.5 cm. The growth intensity of the White Sea harp seal (males) is shown in Table 18.

It can be seen from Table 18 that the increment in the first five years is quite marked (sharp variations are undoubtedly due to the small number of animals measured). Later, however, it is very small and can be perceived only in a series of animals. Similar age variations are seen among females but their growth tapers off slightly sooner (roughly by a year), after which their length increase is very small.

Molting in animals of all later generations, commencing from yearlings, is an extremely perceptible periodic phenomenon in the life of the harp seal; at the same time, it has played an extremely important role in hunting since it serves as a no less powerful impulse than reproduction for the concentration of large numbers of animals in certain periods in relatively small sections of drifting ice floes. Hunters attempt to reach such dense molting rookeries as well as the nurseries. Chronologically, molting follows the periods of parturition, lactation, and mating, extending among the White Sea seals from the last 10 days of March up to mid-May. This period does not cover the duration of individual shedding of the hair coat (which in some animals is much shorter) but the duration of the overall period of molt among animals in a population. The animals setting out to molt initially concentrate in nearly the same areas (or in their proximity) where the nurseries existed quite recently. In the 1960s, the molting nurseries were quite often encountered in the neck region of the central basin of the White Sea. Quite often, especially when access to the basin was delayed, the animals migrated to the northeastern regions of the sea into Mezensk Bay and into the inlet (or collected there). By mid-May the animals departed (or drifted away) from there to the ice floe fringes in the Barents Sea. Sometimes the rookeries were formed opposite the western sections of Tersk coast. In 1964, a large rookery was detected even close to the Karelia coast, in the region of Gridin (M.Ya. Yakovenko).

315 Table 18. Increase in body length (L_c) of the White Sea harp seal (males) in relation to age (Yakovenko *et al.*, 1964*)

Age, years	Number measured	Range, cm	Average, cm	Annual increment, cm
1	8	130-150	138.1	
2	4	152-169	161.0	22.9
3	5	156-172	165.0	4.0
4	6	166-182	174.7	9.7
5	16	170-191	180.9	6.2
6	57	162-196	184.7	3.8
7	70	170-207	186.5	1.8
8	42	162-201	188.6	2.1
9	45	161-205	189.3	0.7
10	14	181-203	192.9	3.6
11	11	185-198	193.4	0.5
12	9	178-200	189.6	3.2
13	3	196-202	199.0	9.4
14	2	200-203	201.5	2.5
15	2	185-190	187.6	-4

316 The seals select various types of ice floes for molting rookeries with the only proviso that they should not drift rapidly toward the open fringes and at the same time provide access to the water. The animals lie along the edges of large- and medium-sized ice floes forming a live border with their bodies lying close together. Such ice floes are separated from each other by narrow or sometimes broad open water pools or partitions or gapes; the animals lie on either side of these, presenting a picture of complex branched strips or bands. Such a deposition is highly characteristic of the early male rookeries. The animals are disposed more haphazardly on the so-called conglomerate ice, i.e., predominantly on small broken ice pressed together by winds or currents and held together by frost.

The density of disposition, the size of the rookeries, their number, and composition vary widely. The animals are sometimes concentrated in a single huge rookery or sometimes divided into several rookeries of much smaller size. Under favorable conditions, a rookery can exist continuously for quite a long time.

An extremely characteristic feature of the molting rookeries is the fluid state of their age-sex composition. The first (excluding pups) to molt are the mature males and the first molting rookeries consist almost exclusively of animals with a wing pattern. At the commencement of April immature animals of both sexes except under-yearlings (gray animals) join them. After shedding the embryonic white coat, the under-yearlings

molt no more in the first year. However, at this time, young animals (aged one to four-five years still preserving infantile coloration) constitute no more than 15%. The proportion of mature females in the rookeries at this time runs into a few percentages but in any case does not exceed 10%.

In the last 10 days of April, the immature animals increase in numbers up to equal those of animals with a wing pattern and the percentage of the adult females slightly rises.

According to the situation prevailing in the 1920s and the 1930s and later (Dorofeev and Freiman, 1928; Surkov, 1957), at the end of April and in the first few days of May, the percentage ratios existing in the molting rookeries between the main constituent animals somewhat reflect the potential ratio characteristic of the herd: adult males and adult females 25% each and immature animals 50%. These figures can hardly be regarded as factual since females predominate among the animals caught. There is reason to believe that the actual position is considerably more complex.

The above age-sex ratios in the molting rookeries at April end to early May represent a regular process observable even at present. It is graphically depicted as the crossing of curves showing the different periods of molt among the different constituent animals of the herd. This is strikingly demonstrated, especially by the data for the early 1960s, when no one doubted the distinct disproportion between the number of productive males and mother animals (Yakovenko and Nazarenko, 1962; Yakovenko, Nazarenko and Timoshenko, 1963; Yablokov, 1962; and others). Consequently, from the equilibrium (or similarity) of the percentage ratios between males and females in the late molting rookeries, no conclusion whatsoever can be drawn about the actual balance between the different groups in a herd.

The final period of the molting rookeries of the White Sea herd was studied less fully since the seals desert the White Sea and hunting ceases. It is usually assumed that the very late rookeries consist mainly of immature animals of both sexes and adult females. However, even in the first of the molting animal concentrations along the fringes of the western part of the White Sea inlet, young ones were in a majority from April 5 (Khuzin, 1970) and observations of the migrating animals point out no perceptible division among them into age groups as the animals advance toward the White Sea (Beloborodov, 1969). Some direct observations (Sivertsen, 1941) also point to a large variation of the composition of the rookeries even in the last 10 days of May.

317 The process of molting is quite prolonged. The old hair coat continues to be sported until the new hairs grow to half the length of those

shed. However, the implantation strength of the older hairs gradually decreases. During molt, whiskers too are shed along with the hairs; evidently claws commence growth at this time. The horny layer of the epidermis is also shed in small and large strips simultaneously.

Some new data available only recently suggest that molting among the various groups of seals entering the White Sea occurs at different times in different regions. It has been found that among an overwhelming majority of the animals residing in the open sea, especially the adult males, molting was at its peak on April 27 while molting of animals arriving later in the inlet region had only just commenced (Khuzin, 1970).

Enemies, diseases, parasites, mortality, and competitors. From among the vertebrates, the potential enemies of the harp seal in water are the Greenland shark (*Somniosus microcephalus*) and the killer whale (*Orcinus orca*) and on ice floes, the polar bear. Raven and arctic fox can also be listed among them. The destructive role of all these animals is extremely variable. The Greenland shark and the killer whale pose the greatest danger to the White Sea herd. However, the shark is confined mainly to the deep sections although it is capable of surfacing and, what is more important, it is generally rare in the White Sea. Seal remnants were detected in the stomach of Greenland sharks caught on Murman and on Kanin Island (Breitfus, 1906; Smirnov, 1935; Andriyashev, 1954). The role of the killer whale has not been supported by actual data since it is not actually caught in the Barents Sea; yet it cannot be ruled out as a potential enemy. In fact, in the eastern part of the sea, especially along the coasts, this whale is encountered extremely rarely during the migration of the White Sea harp seal.

The polar bear, by and large, poses no real danger to the seals of our herd for several reasons. It has not been sighted, as far as people can remember, in the zone of reproduction and is extremely rare in the high latitudes of our western Arctic. Further, the bear has access only to seals on ice floes where the harp seal is almost nowhere seen in the summer.

Foxes can probably attack the newborn but they are hardly even seen in the nursery zones; by the time the rookeries drift toward Kanin Nos, the young one has grown considerably and molted and the fox is no longer capable of attacking it.¹¹² The fox, if it strays onto an ice floe, has to satisfy itself under the best of circumstances with only the frozen placenta.

In this respect, ravens cause serious damage and are often encountered in the nurseries. They feed mainly on the placenta or the dead

¹¹² See: V.G. Heptner *et al.* *Mammals of the Soviet Union*, vol. 2, pt. 1.

pups but, in rare cases, may even attack live pups, primarily undergrown, sick, underfed, and hence incapacitated ones. Regardless, the skeletons of pups with a pecked head have been encountered from time to time in the White Sea rookeries. Sometimes, large gulls also indulge in this activity. In some years the number of dead pups with pecked heads has reached 25% of the total dead pups recorded in a given section of the nursery (Rudakov, 1936). In other years, however, as in 1947, no such instances were reported (K.K. Chapskii). An instance of attack even by ermines has been recorded (L. Popov, 1955).

Among the other more common factors for pup mortality are: (1) 318 defective births (birth with the amniotic sac and placenta) and other instances of still births; (2) freezing and death due to emaciation; (3) crushing by hummocking ice floes; and (4) washing away by waves. Pups in the White Sea perish relatively more often due to the second and third factors though sometimes the first factor as well as the second play a predominant role (Yakovenko and Nazarenko, 1962). The emaciation of a pup transformed into a starveling is caused by the cessation of lactation, due to the loss of its suckling mother. If the pup ceases to receive milk at a weight of less than 15 kg, it cannot survive (Yakovenko and Nazarenko, 1962). Pups whose lactation has been interrupted even somewhat later do not attain normal growth.

The destructive effect of the hummocking of ice floes, which crushes the pups, is very difficult to estimate since the dead ones buried under the vast ice escape attention. Such causes of death can be judged only from instances when the crushed pup is partly visible among the broken ice (or the tracks of the animal are lost under it). Such finds are very rare and do not reflect the true scale of mortality, which is perhaps relatively high since hummocking in the White Sea is a fairly frequent phenomenon.

The washing away by waves of pups which have yet to complete lactation (or their falling into the water while negotiating on the ice floes), causing excessive cooling of the body, is no mean factor in their mortality. However, at present, when the nurseries are formed in the open waters of the White Sea and not close to the fringes (as, for example, in the 1920s), very few pups perish for this reason. In the other locations of the White Sea rookeries, however, such deaths of pups represent one of the most significant factors (N. Smirnov, 1927). Yet situations that prove fatal to the pups do arise from time to time in the White Sea nurseries. One such is when the young ice breaks up intensely during compression and later greatly expands, as happened in 1967 (L. Popov, 1971*). This factor is of equally great relevance to the infant mortality of the

Jan Mayen and eastern Newfoundland (in the "front" zone) populations (Nansen, 1924, and others).

There is yet one more, albeit episodic, very intensely manifest natural factor of infant mortality. In years of anomalous wind directions in the White Sea, when the persistent northeastern and even northern winds prevent the drifting of ice floes into the inlet zone in spring, the well-fed young find themselves carried away by the young ice floes in the opposite direction, i.e., into the western part of the White Sea (Fig. 173). As soon as the ice floes break up and thaw, pups scatter in small groups, at times all along the periphery of the sea, right from the uppermost part of Kandalakshsk Bay to the Onega River and Arkhangel'sk. The weakened and emaciated pups, not finding their natural food, become incapable of independent survival under the unusual conditions and often even crawl to the coasts, thus becoming easy prey to any land predator, even man.

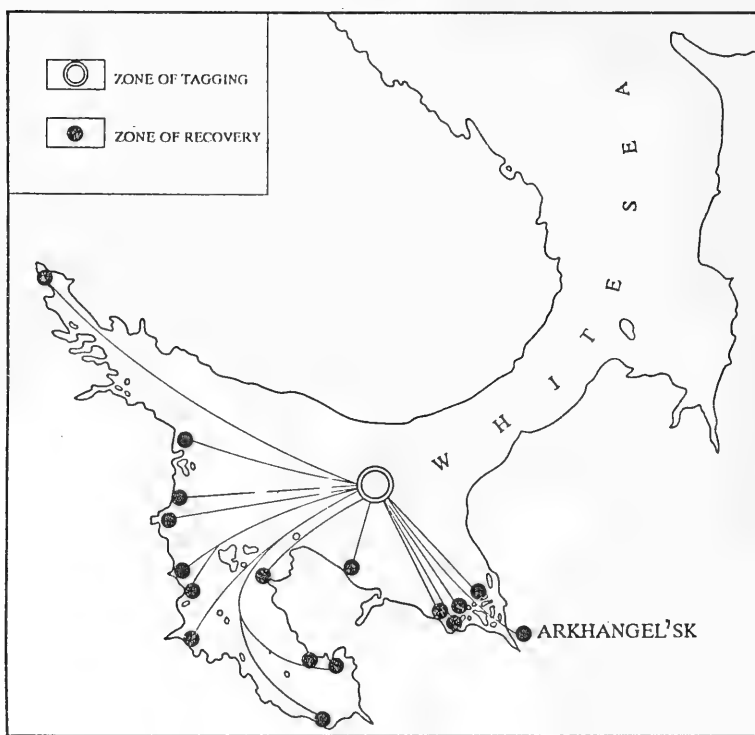


Fig. 173. Some sites of tagged White Sea harp seal pups in 1966 scattered along the periphery of the White Sea (data of the Polar Research Institute of Sea Fisheries and Oceanography, PINRO).

Such a situation prevailed in particular in 1966 and probably led to the large-scale death of pups (Tambovtsev, 1966; Bianki and Karpovich, 1968; Beloborodov and Potelov, 1968). Such instances undoubtedly existed even in earlier times although not very often.

The overall magnitude of the natural mortality of White Sea pups during their residence in the nurseries is not amenable to precise computation since the newborn can be washed off, crushed during hummocking, fall into water, and the dead buried under snow. The figures cited below should therefore be regarded as extremely approximate. For the 1930s, the figures cited at 10 to 11% are slightly exaggerated (Rudakov, 1936) and for the 1940s, on the contrary, the figure of less than 5% is an underestimate (K.K. Chapskii). The actual figure is obviously 5 to 7.5%. The overall mortality of the pups in their first year for the White Sea
 319 herd was taken at roughly 20% in the calculations of population dynamics (N. Smirnov, 1928; P.A. Rudakov, K.K. Chapskii). The mortality in the subsequent age groups has been roughly assumed at 9% in the second year, 6% in the third year, and 5% each in the fourth and fifth years; the average is 7.5% for the mother population and the productive males (K.K. Chapskii). These same indices were used in the latest calculations of the population dynamics of the White Sea harp seal for 1970 (Yakovenko, 1967). For seals of the western Newfoundland herds, the Canadian investigators put the approximate extent of natural mortality in the first year at 50% of the generation (Rasmussen, 1957). The average index of natural mortality for the entire population reproducing in the northeast of the Strait of Belle Isle has been assumed at roughly 15% (Fisher, 1952).

There are no clear references to the diseases they cause but seals do represent a source of disease for the people around them (called "chingi"). When skinning the killed animal to remove blubber, infection of any wound produces an extremely serious inflammatory purulent process [seal finger] leading ultimately to abnormal bone deformation (or damage to the other parts of the limbs).

The helminth fauna of the harp seal has not been studied equally well in all parts of its range. Evidently the helminth fauna was better studied for the harp seal inhabiting the White Sea and in the region of Jan Mayen (Vagin, 1933*; Skryabin, 1948*; Mozgovoi, 1953; Delyamure, 1955; Delyamure, A. Skryabin and Alekseev, 1964*; Delyamure, A. Skryabin and Treshchev, 1965*; Khest, 1932*; Zhvar, 1935*; Stankard and Shoenborn, 1936*). Ten species of helminths and two larval forms are known among harp seals. The trematodes *Orthosplanchnus arcticus* and *Pseudamphistomum truncatum* infect the gall bladder and the bile

ducts of the liver. The cestodes *Diphyllbothrium cordatum*, *D. schisto-*
 320 *tochilus*, *Diplogonoporos tetrapterus*, Diphyllbothriidae g. sp., and others
 are sometimes parasites in the intestine. The nematodes *Contracaecum*
osculatum, *Phocascaris phocae*, *Ph. cystophorae*, Anisakidae g. sp., and
 others infect the stomach and intestine, with as many as a thousand
 present at one time; *Terranova decipiens* is encountered only in the intestine.
 The acanthocephalan *Corynosoma strumosum* infects the intestine
 (V.V. Treshchev).

A comparison of the helminth fauna of the White Sea and Jan Mayen
 harp seals showed that acute differences along with features of similarity
 exist (Table 19). Of the 121 Jan Mayen animals studied (V.V. Treshchev),
 113 (84.8%) were infected. Newborns (seven) were free from helminths;
 however, the yearlings as also almost all animals of other age groups were
 100% infected. The most infected body parts were the stomach (in 91.7%
 of the animals) and the small intestine (87.6%), and less frequently the
 duodenum (29.7%). It was established that five- to eight-year-old White
 Sea harp seals are infected more severely than other age groups. An
 average of 131 helminths were found in the infected animals.

According to the data of investigations covering 169 White Sea harp
 seals (V.V. Treshchev), 95 (56.2%) were infected. Newborns with white
 hair coat and normally molting pups were not dissected for helmintholog-
 ical studies but two of the 72 molted pups (gray ones) aged 1.5 - 2 months
 were found to be infected with immature nematodes. All animals older
 than one year (97), except for two, were infected (97.7%). The seals of
 the White Sea herd were more severely infected with helminths at the
 age of 13 - 16 years. Often the stomach (in 56.2% of the animals) and the
 small intestine (52.0%), and less frequently the duodenum (44.4%) were
 infected. An average of 341 helminths was found, indicating the severity
 of the invasion, which led to the formation of innumerable unhealed
 sores up to 20 mm in diameter on the stomach walls.¹¹³

There are no serious competitors of the harp seal in the White, Bar-
 ents, and Kara seas with regard to food. In the pelagic regions in sum-
 mer, stray ringed seals are sometimes found along with this species on
 the polar fringes. In autumn, in the coastal regions, especially on Novaya
 Zemlya where large masses of polar cod gather for spawning, ringed seal
 and bearded seal appear along with the harp seal. However, they rep-
 resent no competition since fish food is abundantly available there. A
 similar situation prevails later on the northern coasts of the White Sea.
 In the pelagic sections, however, in winter and early spring, other seals

¹¹³ A short review of the helminths of harp seals was made by the staff of the helmintho-
 logical laboratory of Crimea State University under the guidance of Prof. S.L. Delyamure.

320 Table 19. Comparison of the helminth fauna of the harp seals of Jan Mayen and White Sea herds

Helminth	From Jan Mayen region	From White Sea region
<i>Orthosplanchnus arcticus</i>		+
<i>Pseudamphistomum truncatum</i>	+	
<i>Diphylobothrium cordatum</i>	+	
<i>Diphylobothrium schistochilus</i>	+	+
<i>Diplogonoporus tetrapterus</i>	+	+
<i>Diphylobothriidae</i> g. sp.		+
<i>Contracaecum osculatum</i>	+	+
<i>Phocascaris phocae</i>	+	+
<i>Phocascaris cystophorae</i>	+	+
<i>Terranova decipiens</i>	[]	[]
<i>Anisakidae</i> g. sp.	+	+
<i>Corynosoma strumosum</i>	+	+

are not found near the nurseries and molting rookeries. Only the white whale can be seen rather frequently in the large open water pools but predominantly in the central basin; these whales are not, however, seen right within the rookeries.

Population dynamics. Man's hunting activity is almost the lone factor responsible for the population dynamics of this seal. Until the beginning of this century, hunting in the White Sea was relatively low, the herd reduction was much less than the births, and the growth of the herd was therefore good.

In the first 15 years of this century, hunting intensified noticeably and the growth of the herd slowed down as a consequence. From the 1920s, the population began declining sharply and continued to fall almost up to the early 1940s (see pp. 391, 430). During the Great Patriotic War (especially in 1942, 1943, and 1944), further decline in the population was arrested and the herd slightly improved but the 3- or 4-year break was inadequate. The subsequent fresh hunting spree, although not so intense as before 1940, caused further population reduction. From 1965, when the White Sea herds quite clearly became very lean, the use of ships for hunting in the White Sea was banned for five years. An exception was permitted only in favor of the coastal collectives who were assigned the right to hunt for 20,000 pups a year. Additionally, nearly one-half this number was killed outside the White Sea boundaries by the Norwegian hunting fleets.

The sharp reduction in hunting activity stopped the degradation of the herd but the measures did not produce the expected results; the population rose at a slow tempo. By the end of five years' restriction, however, the White Sea population had improved considerably and began to rise; nonetheless, by 1968 the mother seals only slightly exceeded the 1963 strength (M.Ya. Yakovenko). However, the accumulated reserves should promote the growth of the herd. The seal population is regularly controlled by the scientific institutions of the USSR and especially the Soviet-Norwegian Commission for Seal Research in the Northeastern Subarctic and Arctic Atlantic.

The status of the other populations of harp seals, the Jan Mayen and Newfoundland seals, is not so fortunate. The population dynamics are adverse in the case of the Jan Mayen herd, geographically closest to the territorial waters of the USSR and even representing a hunting base for our fleets (see pp. 389-391). The steadily declining numbers of animals caught per ship reflect the significant reduction of reserves. A century before (1866-1870), the average catch per ship was 4,341; at the beginning of this century (1901-1905) 1,400; in 1921-1925, 1,046; and in 1931-1935, fell to 862. Hunting practically ceased in 1941-1945. In the postwar years, in spite of the ban and improved fleet, the catch tended to decline.¹¹⁴

Judging from the results of aerial photographic surveys of the harp seal nurseries in the Newfoundland region, even the Canadian population underwent sharp reduction, with the mother seals in it decreasing by nearly one-half (see p. 391).

Field characteristics. The adult animals in the final phase of the hair coat coloration are easily recognized from the intensely dark wing-shaped patterns on the body standing out in contrast to the light-colored background and also from the head which is as dark as the pattern. Among the animals of transitional type coloration, these dark patches are quite
322 distinct along the body flanks. They are diffuse toward the outer fringe although the wing-shaped patches are of smaller dimensions. The immature animals of both sexes and the very young (infantile type of coloration) gestating or whelping females have fairly distinct contoured, small, dark patches that are sparsely scattered on a gray background.

These seals usually live in herds on the coasts and do not emerge onto stationary coastal ice (fast ice). (K.Ch.)

¹¹⁴ The numerical data were borrowed from R.Sh. Khuzin who processed the hunting statistics published by Sivertsen (1941), Iversen (1927*), and the Norwegian Fishing Directorate.

Economic Importance

The harp seal is of primary importance to hunting. Its potential resources on restoration and subsequent rational utilization would ensure a catch in future (for the population as a whole) of at least 400,000 animals per year for a very long time.

Unfortunately, due to mindless plundering of reserves even in the relatively recent past under pressure of international competition and markets, the reserves of this species of seals had been rather depleted by the middle of the present century. This situation was largely due to the long absence of a reliable census. The numerical data given in Table 20 show the volume of hunting in the past and at present.

323 The advance of the harp seal to first place among the seals hunted was promoted not so much by the very high potential of its population increase (the total actual reserves of the ringed seal are slightly more than the present-day strength of the harp seal), as by the favorable conditions for its hunting. These conditions are: the high degree of concentration in localized sections of the range where these seals form massive and fairly dense groups in rookeries on the ice and are quite accessible even to poorly equipped hunters. With the present organization and hunting techniques, however (powerful icebreakers, better hunting ships, transport and survey helicopters and planes, radio communications, etc.), the high concentration of these seals makes for highly efficient hunting.

The harp seal is caught at present mainly for the fur of the juveniles. An additional raw material is the subcutaneous fat used as medicinal, edible, and commercial fat. The meat portion is used as feed in the farms of fur animals.

The harp seal has long been hunted in the White Sea. The origin of such hunting runs into the prehistoric period. There was regular seal hunting in the Neolithic period, mainly (judging from kitchen remnants) of the harp seal, even in the basin of the contemporary Baltic Sea. In the remote past the seals played a very significant role in the life of prehistoric man at many places by providing him not only with hides and fat, but also edible meat. Until recently, the coastal Eskimos and Chukchis depended almost wholly for their existence on the hunting of the walrus and various seals.

Even at present for people from the south who settled along the White Sea coasts and took to raising cattle and at places cultivation and fishing, sealing (in which the hunting of the harp seal was of exclusive importance) is not the least of their activities. Right up to the beginning of this century (especially in 1901), earnings from hunting the White Sea harp seal in Mezensk district were put at 27,000 rubles and exceeded

322 Table 20. Average number of White Sea harp seal* killed per annum at five-year intervals from 1875 through 1945 (in thousands)

Years	Killed by Russian hunters			Killed by Norwegian hunters			Total average for the period
	Min.	Max.	Average	Min.	Max.	Average	
1875 - 1880	19.3	48.3	30.7	5.6	9.1	7.3	38.1
1881 - 1885	8.9	58.3	26.6	3.1	19.8	9.6	36.2
1886 - 1890	12.9	33.0	19.1	15.8	22.7	19.6	34.8
1891 - 1895	13.3	40.7	23.6	24.1	33.0	28.5	52.1
1896 - 1900	37.0	74.5	57.1	27.1	38.0	34.7	91.7
1901 - 1905	19.3	64.6	33.9	32.5	79.8	57.9	92.0
1906 - 1910	19.2	25.6	21.8	42.6	107.0	76.8	98.7
1911 - 1915	27.7	50.2	46.3	84.5	118.4	99.2	125.6
1916 - 1920	28.0	49.6	37.8	74.9	154.2	106.6	144.4
1921 - 1925	36.4	124.6	70.4	69.0	343.0	188.8	259.3
1926 - 1930	92.5	182.1	140.5	90.7	231.1	167.2	316.7
1931 - 1935	102.1	197.8	141.1	47.1	150.5	108.1	245.1
1936 - 1940	10.1	168.9	95.3	34.1	42.7	37.1	124.9
1941 - 1945	2.7	131.8	55.0	—	—	—	55.0

Calculation based on material compiled by R.Sh. Khuzin, who used such primary sources as Iort and Knipovich (1907) and Siverstsen (1941), whose data included other species as well (their quantum does not exceed 1%); data for the postwar Norwegian statistics (Fish Catch, 1949 to 1959) and Russian statistics.

earnings from salmon fishing (23,000 rubles). A higher income came only from forestry (wood processing and sawing) at 100,000 rubles, agriculture 77,000 rubles, cattle breeding 47,000 rubles, and navaga fishing 34,000 rubles. The income was less from deer farming, river and lake fisheries, hunting in forests, and transport.

The primitive seal hunting on the ice floes in the White Sea was cumbersome and risky in the past and was organized by groups of hunters. The people on the coasts and in Mezensk district called such groups "bursas". For the most part, a group consisted of five to seven hunters in a spacious boat. On the Tersk and Karela coasts, these groups (called "romshas") comprised only a few people. When the rookeries began forming, the "bursas" set out with their paraphernalia for the sea ice. Dragging heavy boats, experiencing quite some hardships, and exposed to danger, the hunters wandered in search of the rookeries for many days. It was most risky to land on drifting ice floes singly or in twos or even threes (without boats) while chasing the seals sighted from the coasts. It was necessary to hurry back, towing the hides and the blubber, to negotiate the island before the ice broke apart excessively.

The first Russian ships began being detailed for seal hunting in the White Sea right at the beginning of this century but group

hunting continued until the Revolution and after. From the 1920s to the 1930s, most of the hunters from the coastal collective farms engaged icebreakers which, in the 1920s - 1930s as well as in the postwar years, carried out state hunting operations in the White Sea. Apart from the icebreakers, special hunting ships were recruited. On the whole, hunting, regularly assisted by reconnaissance planes, was more intense.

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The White Sea harp seal was killed in the largest numbers (exceeding 300,000 annually) for five years from 1924 through 1928. In the next five-year period (from 1929 through 1933), the average annual kill dropped to 250,000, and still later from 1934 through 1938, fell further to 188,800 on average. There is no doubt that hunting in the 1920s was extremely intense. The average annual kill in the postwar years steadily fell as follows:

1946 - 1950	166,300
1951 - 1955	151,700
1955 - 1960	115,000
1961 - 1965	81,900

Norwegian hunting ships also cruised along with our hunting operations in the White Sea region and in the adjoining southeastern sections of the Barents Sea. Before the end of the 1930s, the Norwegian hunters were given a concessional right to hunt for the harp seal in the northern part of the White Sea (north of the line joining Capes Orlov and Konushin). At the end of the Great Patriotic War, the agreement was not renewed and at present the Norwegian hunters hunt outside the White Sea limits and in the adjoining areas in a few dozen small hunting boats. Hunting is regulated by agreements.

From the second half of the 1960s, the organization of our hunting activity in the White Sea underwent radical change. In the five years ending with 1969, state hunting ceased because of the depleted reserves. Neither icebreakers nor special hunting ships carried out hunting in the White Sea. An exception was made only for the local collective farms, which were given the right to hunt 20,000 pups a year. The collectives rented helicopters to reach the hunters on the ice and transport the killed animals to the coastal base. No more than 10 days were spent in the entire hunting operations under favorable conditions.

Until recently, well-fed normally molting young animals were brought onto the coasts where they were allowed to complete molt in special enclosures on land.

The Norwegian hunters in the immediate proximity of the White Sea inlet area caught no more than 14,500 animals per annum in the 1960s (Table 21), mainly the older juveniles and adults. It was thought prudent to maintain the hunting level as at the end of the 1960s in

the next decade to promote a more rapid population recovery. After a short period of relative restriction, the population had not reverted to the level of the 1920s and 1930s (the year 1925 was a record for the White Sea region; Soviet hunters caught 124,600 animals and the Norwegians 343,000 animals, i.e., slightly less than half a million seals). The ban imposed in 1963 on killing adult females in the nurseries had an extremely salutary effect in restoring the White Sea population.

The technique of hunting in the nurseries was extremely simple in the past. The hapless white pups could not escape from the hunter and were killed directly using clubs. Since suckling mothers usually do not leave their pups, "hunting" them also posed no problem. Nevertheless, rifles were used to kill them. In the past, hunting in the molting rookeries was more complicated. Hunters with harpoons [rifles] approached quietly in white masks and aimed from behind cover. The shots frightened the sleeping animals and soon only dead animals remained on the ice floe. In some cases, when the ice floes became compact (usually in high tide), open water pools disappeared and the ice lumps filling them froze and the animals were thus cut off from the water. Hunters could then kill them even with clubs. Usually, however, even in compact frozen areas, the animals could ultimately get into the water by pushing aside the ice lump or pressing it with their bodies.

Table 21. Harp seals (White Sea population) killed in the postwar years (in thousands)
(after R.Sh. Khuzin)

Year	Killed by Soviet hunters	Killed by Norwegian hunters	Total killed
1946	79.1	8.5	87.6
1947	161.1	6.6	167.7
1948	146.3	8.9	155.2
1949	183.4	25.1	208.5
1950	194.7	17.7	212.4
1951	192.2	33.8	226.0
1952	131.4	19.1	150.5
1953	88.3	12.4	100.7
1954	152.8	11.6	164.4
1955	97.8	19.1	116.9
1956	68.0	25.1	93.1
1957	107.9	22.3	130.2
1958	119.6	15.1	134.7
1959	101.4	8.5	109.9
1960	95.9	10.7	106.6
1961	93.8	11.2	105.0
1962	106.9	8.3	115.2
1963	69.5	13.3	82.8
1964	62.7	14.6	77.3
1965	20.1	6.4	26.5
1966	20.0	12.2	32.2

The first of the denser rookeries of males with a "winged" pattern and disposed in rows along the edges of open water pools and fissures (Fig. 174) are the least accessible to hunters. It is difficult to approach the animals within the required distance as they abandon the ice floe at the first shot and dive pell-mell into the water.

The killed animals are processed very quickly: first a cut is made along the abdomen from head to tail, next circular incisions made through the skin with the fat layer around the base of the flippers, and then the subcutaneous fat separated from the muscles. The skins with the fat upward are spread out on the ice and stacked for loading in a vessel that comes later. Nowadays, the extensive use of airplanes and killing pups exclusively has made the job quite simple and fast. At the coastal base the fat is separated from the skin, the skins degreased to the maximum possible extent, and salted. In the natural or even dyed form, the white embryonic pelage and now, more so, the skins of the molted gray pups are in great demand in the internal and well as international markets.

Drifting ice floes in the region of Jan Mayen Island represent another region of hunting. Exploitation of this international hunting zone began over 200 years ago. The maximum intensity of hunting in Jan Mayen was recorded in the 1870s (200,000 seals were killed there in 1874). The decline in killing began subsequently, touching the lowest level at the end of the first 10 years of this century. World War I interrupted the



Fig. 174. Early spring rookery of adult males. White Sea, April 18, 1966 (photograph by Yu.I. Nazarenko).

hunting activity and this helped the herd to restore itself to some extent. After the war, hunting resumed and reached a fairly high level.

World War II again interrupted hunting activity but it was rapidly resumed thereafter and, in the first half of the 1950s, exceeded the prewar level. On average, the kill in the first five years of the 1950s was 39,300 seals with a very large number of modernized vessels operating. However, the success was short-lived and unreliable. The pressure on the animal population was excessive and it rapidly declined; an index of this decline was the reduction in the number of animals killed per ship (see Table 22). The lowest annual yield for the entire hunting duration in this century occurred in the first half of the 1960s (average kill per ship fell to 467 seals in one expedition although the vessels had been equipped with new diesel motors) (R.Sh. Khuzin).

Soviet ships began hunting in the ice floes of Jan Mayen Island region in 1955 and continued hunting there until 1965 (see Table 23). Hunting was discontinued as it was unprofitable.

The commercial exploitation of the Newfoundland populations by the local people, in which the USSR became somewhat interested in the 1960s, began almost concurrently with hunting of the White Sea resources. Hunting of harp seals using ships had begun there at the end of the eighteenth century and reached an immense scale of 500,000 a year in the 1820s. Hunting continued at this level for forty years (Allen, 1880).

Table 22. Norwegian hunting of the harp seal in the Jan Mayen Island region from the 1880s (after R.Sh. Khuzin)

Years	Average annual kill, thousands	Average number of expeditions per ship per annum	Average kill per ship expedition, numbers
1881-1885	82.8	17.5	5,241
1886-1890	33.3	22.8	1,469
1891-1895	45.8	19.6	2,338
1896-1900	24.3	12.4	1,960
1901-1905	15.1	10.8	1,400
1906-1910	14.0	21.6	648
1911-1915	17.4	29.2	596
1916-1920	32.3	59.7	542
1921-1925	19.5	18.6	1,046
1926-1930	32.6	33.5	969
1931-1935	32.3	37.4	862
1936-1940	36.7	45.6	803
1941-1945	—	—	—
1946-1950	36.1	37.0	976
1951-1955	39.2	55.6	859
1956-1960	25.0	39.8	585
1961-1965	18.6	39.8	467

Table 23. Jan Mayen harp seals killed by Soviet hunting ships in the 1960s (after R.Sh. Khuzin)

Year	Number of hunting ships	Total killed by all ships, number	
		Total	Pups
1960	8	3,356	420
1961	8	6,043	755
1962	8	2,423	303
1963	7	1,977	222
1964	8	4,483	560
1965	8	6,273	896

One can well conjecture the original population level of the local harp seals to be able to sustain such a prolonged and intense rate of hunting. By the end of the nineteenth century, the number of animals killed had fallen to half in spite of maintaining the same intensity of hunting; in the first few decades of this century, the number decreased even further, to 160,000 a year.

World War II served as a fortuitous interlude that extended for sometime after the war. The continuous interruption of hunting using ships undoubtedly promoted a partial recovery of the animal population. But hunting resumed in the 1950s and exceeded the prewar level, with the annual kill reaching 262,000 (Fisher and Sergeant, 1960*). At the present level of the animal population, given such large kills the animal population can hardly restore itself to the original level.

At the beginning of the 1960s, hunting was carried out in the Newfoundland region twice on a trial basis by Soviet hunters. As it proved unprofitable and Canada extended its coastal waters to 12 miles, the Soviet Union ceased hunting in the Newfoundland region.

At the end of the last century and in the first thirty years of this century, this seal was also caught in nets. This was mainly practiced by the locals off Murman but here and there the White Sea harp seal was caught even in the White Sea before total icing set in. Catching in nets was quite profitable off Murman. For example, at Kharlovka about 1,000 seals were thus caught from the end of winter to early spring in 1898-1899.¹¹⁵ This hunting practice flourished even in the 1920s (Skvortsov, 1927). Nets were no longer used in subsequent years off Murman mainly because the seals changed their approach to the Murman coast.

Sighting the harp seal on the Murman coasts, people unjustifiably assumed its adverse effect on the catch of cod there. Even very old reports

¹¹⁵ See: Proceedings of the Murman Scientific-Hunting Expedition, St. Petersburg, 1912.

contain frequent references to the fatal consequences of the presence of seals on the Murman fishing industry. Thus, in 1801, the seals reportedly "chased away the entire fish from the Murman coast" right up to Rybach'ii Peninsula. In 1803, the "catch was good from the spring but kozha¹¹⁶ arrived in summer and chased away the entire cod". In 1807, "right from the spring, kozha spread all along the coast like tree stumps in a forest, as a result of which the fishermen could not catch even a single fish". Similar complaints were registered in subsequent years (Reineke, 1830*). In fact, the White Sea harp seal continued to be accused for quite some years, often with even greater exaggeration.

328 The accusations that the harp seal consumed large quantities of commercial fish, especially cod, or chased it away were never confirmed. On the contrary, the arrival of cod was usually not accompanied by the arrival of seals; instead the absence of cod coincided with the arrival of the White Sea harp seal. Thus the cod *per se* holds no attraction for the seal (N. Smirnov, 1924); this is explained by hydrological conditions. The harp seal is a distinct element of the arctic fauna; it is sensitive to the thermal regime of the water (even early in this century it served as an indicator of the cooling of the water or of the invasions of arctic waters (Linko, 1912)). Thus, instances of the temporary disappearance of the relatively thermophilic cod on the Murman coast and the simultaneous appearance there of the White Sea harp seal were actually impelled by cooling or ingress of arctic waters.

The harp seal of the White Sea herd is one of the most harmless species of seals in relation to the fishing industry, coming in third place after the bearded seal and the walrus among the Pinnipedia of the North Atlantic. (K.Ch.)

Subgenus of Ribbon Seals

Subgenus *Histriophoca*

RIBBON (BANDED) SEAL¹¹⁷

Phoca (Histriophoca) fasciata Zimmermann, 1783

1783. *Phoca fasciata*. Zimmermann. Geographische gesch. des Menschen u. der allgemein. verbeit vierfüssigen Thiere, 3, p. 277. Kuril Islands.

¹¹⁶ "Kozha" is a local term used by the coastal people for the harp seal.

¹¹⁷ Krylatka—adult animal; belek—newborn pup; and serka—under-yearling after casting the juvenile hair coat.

1831. *Phoca equestris*. Pallas. Zoogr. Rosso-Asiat., I, p. III. Kuril Islands, Sea of Okhotsk ("Rarissime in mari Ochotensi, frequentius circa Curilorum insulas. . ."). (V.H.)

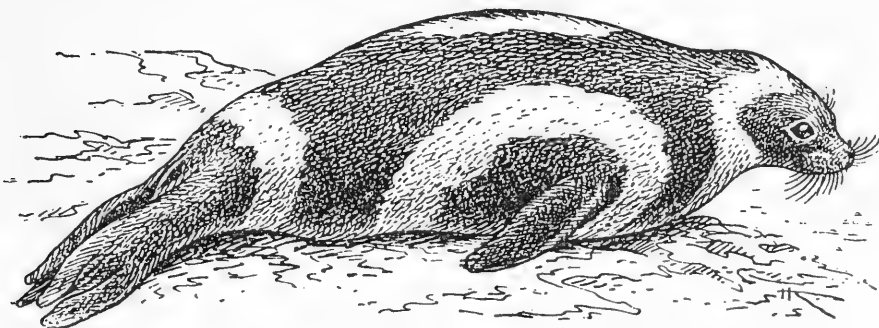
Diagnosis

Four light-colored transverse bands run along the generally dark background of the trunk (Fig. 175). The labial whiskers number 41-42 and orbital whiskers 6-8. The whiskers at the tip of the snout have a wavy surface (Fig. 176). The first digit on the fore flippers is longer than the rest. The paired air sac joined with the trachea is well developed among males (Fig. 177). (V.A.)

Description

These are seals of moderate dimensions [up to nearly 2 m in length]; the males are usually larger than the females.

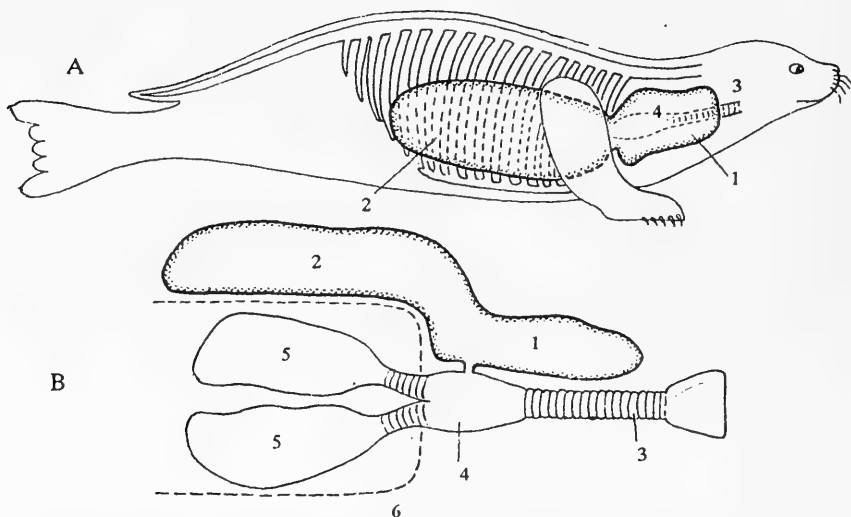
Body long, streamlined. The color of the adults is typical: four light-colored bands run along the dark background (black or brown among males; brown or brownish-gray among females). One band encircles the neck like a collar, covering also the rear portion of the head, and another



329 Fig. 175. Color of the adult ribbon seal (banded seal), *Phoca (Histriophoca) fasciata* (figure by N.N. Kondakov).



329 Fig. 176. Whiskers of the ribbon seal (banded seal), *Phoca (Histriophoca) fasciata* (figure by N.N. Kondakov).

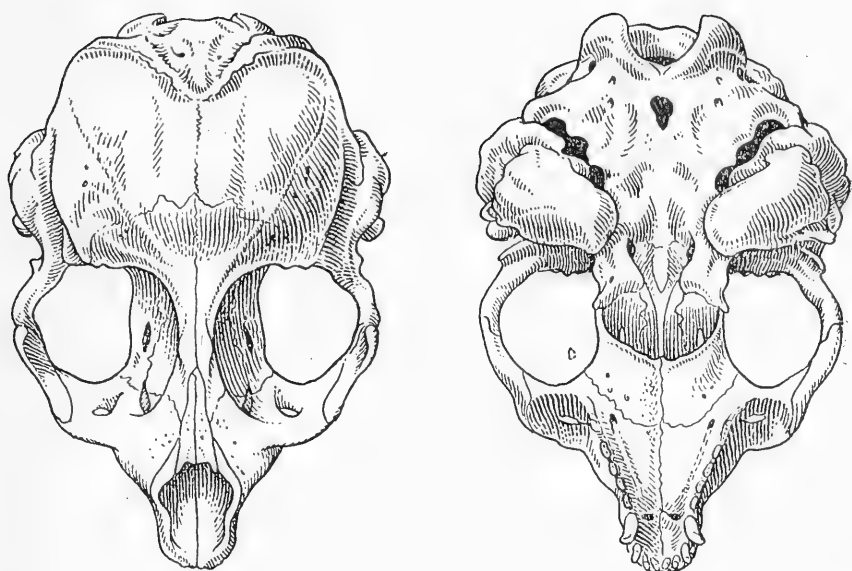


329 Fig. 177. Air sac of the ribbon seal, *Phoca (Histriophoca) fasciata* (figure by N.N. Kondakov). A—general view of air sac filled with air (seen from the right); B—sketch of respiratory tract in the ribbon seal. 1—cervical section of air sac; 2—trunk section; 3—trachea; 4—enlarged section of lower trachea; 5—lungs; 6—thoracic cage (after M.M. Slepstov).

encircles the body at the base of the hind flippers; two symmetrical bands mark the outline of the base of the fore flippers. From a distance, these
330 flippers look like the attached wings of a bird. The width of each band is 5.5–15 cm and its color varies from pure white to yellowish. Fine mottling is sometimes seen on the light-colored bands of young animals. There is no seasonal variation in coloration. (Age-related color variations are described under “Growth, Development, and Molt”).

The skull is shortened and broad, the cranial portion and zygoma broad, the facial portion short and narrow (Fig. 178). The nasals are short, on average 36.6 mm. The bony nasal septum does not reach the posterior margin of the bony palate. The length of the palatine bones is usually less than their maximum width. The tympanic bullae are large (about 33.5% of the condylobasal length), their width considerably less than their length, and set sharply inclined toward the longitudinal axis of the skull. The alveolar margin of the upper jaw is curved; the lower jaw is curved with a downward convexity corresponding to the curvature of the upper tooth row (Fig. 179).

The teeth are small and number 32–36. The canines are small and obtuse, the incisors weak, slightly curved, almost vertical. The molars and premolars are small, set wide apart, their roots tending to fuse. The



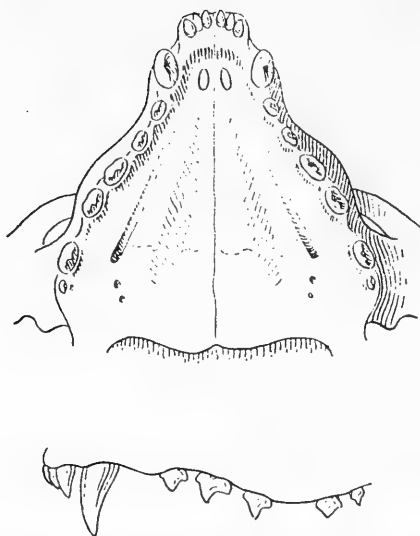
330 Fig. 178. Skull of the ribbon seal (banded seal) *Phoca (Histriophoca) fasciata*
(figure by N.N. Kondakov).

only accessory cusp, located posterior to the base of the last tooth, is most often in the form of a faintly recognizable denticle.

The average body length varies from 155 to 165 cm depending on the age composition of the sample). The maximum length of the male (Bering Sea) is 192 cm, of the female 198 cm (males, however, are generally larger than females). The length of the os penis may reach 150 mm.

331 The condylobasal length of the skull in males averages 191.7 mm, in females 190.7 mm; mastoid width in males 125.1 mm, in females 121.4 mm; length of the upper tooth row in males 57.5 mm, in females 59.0 mm (Ognev, 1935; S. Naumov and N. Smirnov, 1936; Chapskii, 1955, 1963; Shustov and Yablokov, 1967).

The maximum weight of these seals is 150 kg, the average being 55 kg. The average weight of the blubber (fat with hide) is 20 kg and the subcutaneous fat layer is 2-4.5 cm thick. The weight of the os penis is about 20 g. The weight of the internal organs of mature animals is as follows (g): heart 499-513, lungs 978-1,030, liver 1,378-1,403, stomach 401-441, intestines 1,351-1,433, and kidneys 123-144 (A.S. Sokolov *et al.*, 1969). The mode of life of the ribbon seal outside the icy season is not known and hence there is no information on the seasonal changes in weight. (V.A.)



330 Fig. 179. Bony palate and teeth of the ribbon seal, *Phoca (Histriophoca) fasciata* (figure by N.N. Kondakov).

Taxonomy

The ribbon seal is distinguished in the family by its specialized pelagic mode of life, which has led to some characteristic structural features. Some authors (Ognev, 1935; Simpson, 1945; Chapskii, 1963) regard the ribbon seal as a monotypical genus, while others (S. Naumov and N. Smirnov, 1936) combine it in the same genus as the harp seal, with which the ribbon seal shares several common morphological and ecological features and evidently has a common ancestor, although the genesis of the latter is not clearly known. (V.A.)

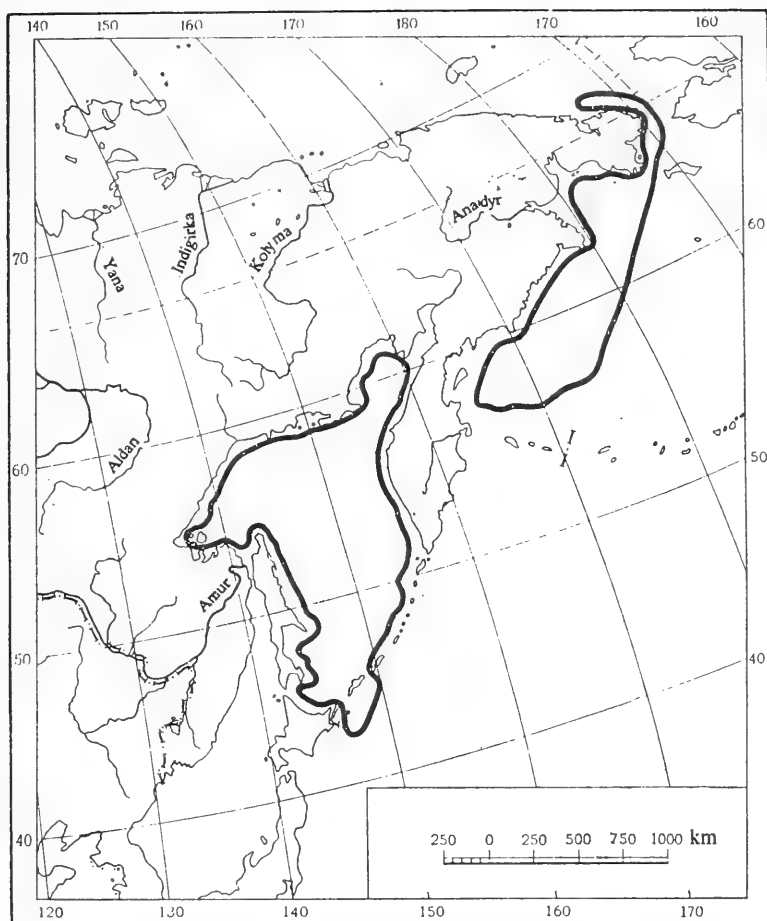
332

Geographic Distribution

Seas of the northern Pacific Ocean—Sea of Japan, Sea of Okhotsk, Bering Sea and Chukchi Sea. Endemic to this section of the world oceans.

Geographic Range in the USSR

Divided into two isolated portions, i.e., Sea of Okhotsk and Bering Sea (Fig. 180). In the Sea of Okhotsk this seal is encountered on the spring ice floes from La Perouse Strait to the Shantarsk archipelago and Shelikhov Bay. the southern boundary runs along the northern part of Tatar Strait (Dorofeev, 1936) and into the coastal waters of the northeastern



331 Fig. 180. Distribution of the ribbon seal (banded seal), *Phoca (Histriophoca) fasciata* in the USSR (V.A. Arsen'ev).

coast of Hokkaido Island (Nishiwaki and Nagasaki, 1960; Nishiwaki, 1966). Distribution in the Bering Sea covers the coastal waters of Koryak Land from Olyutor Gulf in the north, Gulf of Anadyr, Bering Strait, and the Chukchi Sea to Kolyuchin Bay in the west (Shustov, 1965).

Geographic Range outside the USSR

Eastern part of the Bering Sea from Bristol Bay to Bering Strait and waters of the Chukchi Sea to Cape Barrow in the east (Scheffer, 1958; Shustov, 1965).

The southern boundary in the Bering Sea runs from Olyutor Gulf northeast roughly up to 60°N lat., from there eastward and then south-east up to Bristol Bay (Fig. 181). The southern limit does not cross the islands of the Aleutian range (Allen, 1880). The northern boundary runs at places between the Chukchi Peninsula, Alaska, and Wrangel Island from Kolyuchin Bay to Cape Barrow. (V.A.)

Geographic Variation

The southwestern boundary of distribution of the ribbon seal in the Bering Sea lies more than a thousand miles away from the northeastern boundary in the Sea of Okhotsk. The existence of two local populations is thus highly probable. All the same, geographic variation has not been established. (V.A.)

Biology

The mode of life of the ribbon seal is known for a comparatively small duration of the year, i.e., at the time of spring-summer rookeries on the

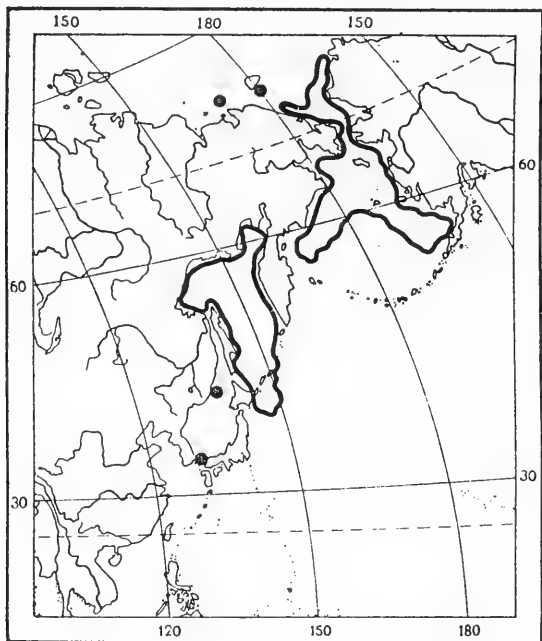


Fig. 181. Species distribution of the ribbon seal (banded seal), *Phoca (Histriophoca) fasciata*. Dots represent sites of records of the ribbon seal (V.A. Arsen'ev).

ice floes. From this viewpoint, it is one of the poorly studied species of Pinnipedia of the Northern hemisphere.

Population. An idea of the population of the ribbon seal in the Sea of Okhotsk was provided by the data of the annual catch, aerial surveys, and observations from ships used for hunting. The total population was thus put at a few tens of thousands. No special census was undertaken. The
333 abundant population of the Bering and Chukchi seas began attracting hunters only in 1961. Calculations based on the areas of ice floes, density of disposition of seals on various types of ice floes, and aerial and visual observations put the total strength of this population at 80,000 to 90,000 (Shustov, 1969).

Habitat. These seals generally select firm, clean, white hummocky ice blocks invariably with an even surface for their spring-summer rookeries. Instances of finding these seals on dirty ice blocks are very rare and are possible at the end of the icy period when the area of the ice floes has greatly diminished. The height of the ice floes is not of much consequence as the seal can jump onto an ice block 1 m or more in height. The main rookeries are disposed on drifting ice floes far away from the coasts but usually overlying depths not exceeding 200 m. The seals are also sighted in coastal waters but only in the case of early thawing of ice floes. Outside the icy period, the seals evidently lead a pelagic mode of life since they never emerge onto the coasts (barring extremely rare cases). The present sites of distribution of the seals have not been established.

Food. Data on the food of the ribbon seal have been collected exclusively for the period of their residence in the rookeries on the ice floes with no information at all available outside this period. Most of the dissected stomachs in all the regions of study were found to be empty. Thus, 91.6% of 443 stomachs dissected in the Sea of Okhotsk were empty (Pikharev, 1941); in another case, 82% of 398 stomachs were devoid of food (Arsen'ev, 1941); in the Bering Sea, 97.4% of 1,175 stomachs dissected were empty (Shustov, 1965). Based on these data, it was earlier thought that the ribbon seal did not feed in the icy period but thorough investigations established that the intestine of many seals contained food remnants while the rectum was packed with fecal matter. Very rapid food digestion is evidently characteristic of this seal.

In addition to the items listed in Table 24, the stomach of seals in the Sea of Okhotsk at one time contained the bone remains of navaga (Freiman, 1936b) and mysids (Nikulin, 1937b). In the Sea of Okhotsk as well as in the Bering Sea, some stomachs revealed the feathers of sea birds, sand, and stones.

The geographic variation of the food of ribbon seals was quite significant but data for the Sea of Okhotsk (V.A. Arsen'ev, 1941) are clearly

inadequate. The age-related food variations are: young animals (primarily the under-yearlings) feed mainly on pelagic invertebrates (amphipods, mysids and isopods) while adults feed on benthic and pelagic forms in spite of the fact that the depths in the regions of their habitat reach 50 to 100 m or more.

Home range. The ribbon seal does not form large rookeries on ice floes but lives singly or sometimes in twos or threes. There are no distinct male or female rookeries. These seals are seen only on ice floes with a density of predominantly four to six points.

Hideouts and shelters. These seals do not make air holes or snow shelters.

Table 24. Food items of ribbon seals (Shustov, 1965a)

Food item	Number of cases		Percentage of number of stomachs with food remains	
	Sea of Okhotsk	Bering Sea	Sea of Okhotsk	Bering Sea
CRUSTACEANS				
<i>Crangon dalli</i>	1	—	2.0	—
<i>Nectocrangon lar</i>	—	3	—	9.4
<i>Pandolopsis</i> sp.	—	6	—	18.7
<i>Pandalus borealis</i>	—	8	—	25.0
<i>Pandalus goniurus</i>	5	1	9.8	3.1
<i>Eualus gaimardii</i>	—	6	—	18.7
<i>Spirintocaris murchiei</i>	—	1	—	3.1
<i>Lebbeus</i> sp.	—	3	—	9.4
<i>Temisto</i> sp. (2 species)	—	6	—	18.7
<i>Stilomysis grandis</i>	—	2	—	6.2
Amphipods	—	4	—	12.5
Cephalopod mollusks	24	5	47.0	15.6
FISHES				
Polar cod, <i>Boreogadus saida</i>	—	4	—	—
Atlantic herring, <i>Clupea harengus</i>	—	2	—	6.2
Pacific navaga, <i>Eleginus gracilis</i>	—	2	—	6.2
European smelt, <i>Osmerus eperlanus</i>	—	1	—	3.1
Stout eelblenny, <i>Lumpenus medius</i>	—	4	—	12.5
Alaska pollock, <i>Theragra chalcogramma</i>	47	—	92.1	—
Capelin, <i>Mallotus villosus</i>	1	2	2.0	6.2
Common sand eel, <i>Ammodytes hexapterus</i>	—	1	—	3.1
Smooth lumpsucker, <i>Aptocyclus ventricosus</i>	1	—	2.0	—
Pacific cod, <i>Gadus morrhua macrocephalus</i>	4	—	7.8	—

Daily activity and behavior. The number of stomachs with food remnants was 20% more among seals caught during the night, suggesting a more active feeding at night (Shustov, 1965). No other data are available on daily activity.

In cloudy weather, many seals are seen resting on ice floes in the morning and evening hours while most of them remain in water at noon. In rainy weather most seals prefer to be in water and rarely venture onto the ice. On quiet, sunny days the seals almost do not enter the water in the day but gather there in the evening hours and at night. A large number of seals remain in water at night, roughly between 8:00 p.m. and 4:00 a.m., regardless of weather conditions (Pikharev, 1941; Shustov, 1965b).

334 The ribbon seal very easily negotiates ice floes with long leaps, without touching the edge of the floe. It lies quite close to the edge, quite often on a level surface at the foot of a hummock with its head invariably toward the water. It is extremely sensitive and approaching it without detection is very difficult. If, however, a boat with the motor switched off runs straight toward the animal and the people in the boat remain quiet, the seal carefully surveys the boat and permits its approach within rifle shot without attempting to escape into the water. Probably its auditory faculty is poorly developed compared to vision. An injured seal attempting to reach the water quickly, will invariably stop and howl sharply, which the hunter promptly takes advantage of. The animal moves rapidly on the ice floe, contorting its body like a snake, dives almost noiselessly, without a splash, moves far away in the water, and never surfaces immediately. A badly wounded animal attempts to return to a block of ice while a slightly injured one can fiercely attack the hunter (Pikharev, 1939, 1941). Sometimes, for no reason at all, the seal begins to move rapidly on the ice floe from one side to the other, rolling and turning from one side to the other, then rushes suddenly into the sea, only to return immediately to the ice floe with a leap. The motive for these actions is not clearly understood; they resemble playful acts although done singly, without a companion.

335 *Seasonal migrations and transgressions.* Information on migrations is practically not available. In the rookeries on the ice floes, the seals are mainly passive and the movements they do make can hardly be regarded as migratory. On the spring ice floes in the Sea of Okhotsk, the largest concentrations are noticed south of Tauisk Bay, in the region of Iony Island, north and east of Sakhalin. At the end of the icy season, herds of these seals migrate into the region of Shantarsk Islands and into the Gulf of Sakhalin. They are distributed on the ice floes, in patches. In relatively nearby regions on the ice floes, appearing almost identical externally, some will be occupied by the animals and others vacant, the

occupied and vacant floes alternating. Possibly, this is associated with the depths of the region and hence the chances of finding food (Shustov, 1965b). With the thawing of ice floes in the Sea of Okhotsk and the Bering Sea, the ribbon seal disappears. Its summer residence has not been established. Only some stray observations have been reported on the migrations of some seals through the Bering Strait in spring to the north and in autumn to the south (Shustov, 1965b; Tikhomirov, 1966).

Some distant transgressions of the ribbon seal are known. Early September, 1927, a seal was killed in Vladimir Bay in the Sea of Japan (about 44° N lat.) (Pikharev, 1941). In another case, an adult ribbon seal was noticed on June 17, 1944, in Tsushima Strait ($35^{\circ}10'$ N lat. and $130^{\circ}34'$ E long.) 45 miles from the coast (Vedenskii, 1950). Transgression of the seal was noticed into the western part of the East Siberian Sea (Ognev, 1935) and toward Wrangel Island. A male ribbon seal, 131 cm long, was caught on November 16, 1962, close to Morro Bay in California. Its body was devoid of a hair coat except for the vertical surface of the fore and hind flippers, head, and upper portion of the neck. The animal was kept in an aquarium where it died a month later (Aryan [Roset], 1964).



335 Fig. 182. Female ribbon seal with a newborn. Bering Sea (photograph by A.P. Shustov).

Reproduction. The period of whelping extends from March end to early May. In 1962, mating was noticed for the first time in the Bering Sea on March 29 while newborns were encountered on May 2-3, 1963. Mating takes place soon after parturition and thus gestation extends for about a year. Most of the females are capable of producing an offspring every year. Females attain sexual maturity at two to three years of age and males a year later at three to four years. Females older than five years are the most productive. The upper age limit for productivity has
 336 not been established nor has any climacteric period been detected among females. The intensity of reproduction is quite high and the number of gestating females in some years varies from 30 to 60% or more of the total number of females in the population (Shustov, 1965b).

Growth, development, and molt. The ribbon seal is characterized by a latent period of embryonic growth [delayed implantation], roughly calculated as 2.5 months. The newborn averages 85 cm in length, i.e., about one-half the length of the mother. It reaches this length roughly after nine months of uterine development. The average weight of the pups is 8.6 kg. The pups are covered with a long, soft, silvery-white embryonic coat with smoky spots; this coat is sported for about two weeks. In this period the pups feed on the mother's milk. At 25 to 30 days of age, the molted pups (normally molting pups and gray pups) measure an average length of 112 cm and weigh 28.3 kg. The hair coat is short and coarse, slaty on the back, gray on the flanks, and light gray on the belly. After the first molt a dark band with sharp outlines appears on the generally monochromatic dorsal background. At two years of age the white bands characteristic of adults are seen for the first time (Fig. 183). At this age the female acquires the adult coloration while the male of two (or sometimes three) years of age most often is very dull colored like the adult female. Males acquire the adult vividness at 3-4 years of age.

The intense growth of seals in the first few years slows down after maturity. Growth cessation among females occurs evidently at seven to eight years of age and among males at 7-9 years. By this time the seals are fully grown. Females lag behind the males in growth though not very significantly (Table 25).

The longevity of the ribbon seal has not been established. The oldest male studied was 27 years while two females were 26 years old. These animals did not give the impression of senility (Shustov, 1965b; Shustov and Yablokov, 1967; Tikhomirov, 1968).

Shedding of the embryonic hair coat constitutes the first molt, the signs of which are noticed 7-10 days after birth. The hairs are initially shed from the head and the hind flippers and later from the other sections

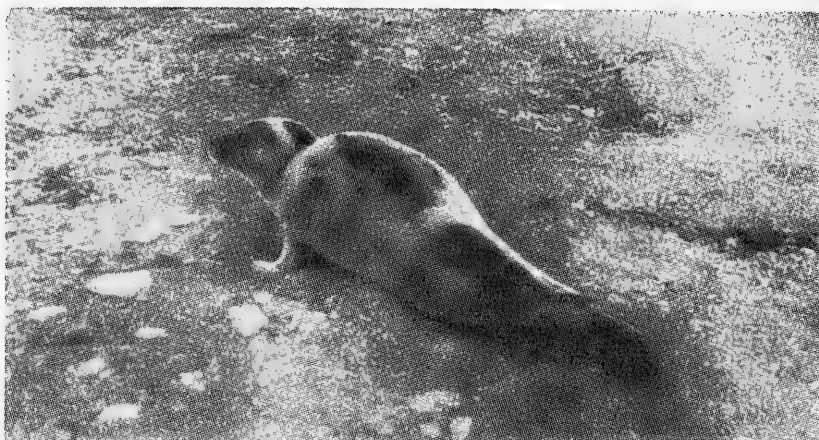


Fig. 183. Young ribbon seal. Bering Sea (photograph by A.P. Shustov).

Table 25. Variation in body length of seals with age (measured along the dorsal surface) (Tikhomirov, 1968)

Age, years	Males		Females	
	No. of animals measured	Average length (cm)	No. of animals measured	Average length (cm)
1	16	132.0	21	129.0
2	20	145.0	22	145.0
3	29	155.0	26	152.0
4	33	156.6	28	153.9
5	17	165.0	22	160.2
6	20	158.9	15	161.5
7	17	160.1	16	168.0
8	19	161.0	5	169.0
9	16	168.1	16	163.9
10	21	163.8	10	163.0
11	13	165.0	—	—
12	14	167.7	19	163.9
13-14	22	165.2	—	—
15-17	26	168.7	12	168.8
18 and above	15	163.1	13	168.1

of the body. The juvenile coat is preserved for quite sometime in the armpits of the fore flippers. Molting ceases roughly at two weeks of age.

The molting of adult seals extends for quite a long period. The second half of April can be regarded as the beginning of the molting period but the cessation of this period has not been established. A ribbon seal caught in the Sea of Okhotsk on May 16, 1939, was at the peak of

molt while another one caught on May 20, 1938, was found to be fully molted. In mid-July, molting animals were seen among those that had already completed molt. The duration of molting can be roughly put at three months. During molt, not only a change of the hair coat occurs, but often a simultaneous and intense peeling of the epidermal layer (Pikharev, 1939, 1941).

Enemies, diseases, parasites, mortality, and competitors. The ribbon seal has practically no enemies in the icy period. Only on occasion does it fall prey to the killer whale, polar bear, or even a large Greenland shark. No information is available on the subject outside this period although there is undoubtedly greater possibility of death being inflicted by the killer whale or shark. Diseases suffered by ribbon seals have not been studied but sometimes animals with skin diseases are encountered. Such animals are partly or even wholly devoid of hair coat, their epidermis is peeled, and bleeding cracks are seen in the affected sections of the skin (a seal in this state was caught in California). The mobility of such animals is greatly reduced and they do not fight man. A blood analysis of three sick seals gave an erythrocyte sedimentation rate of 18 to 25 mm/hr versus 3-4 mm/hr for healthy animals. Such seals, though few, are nevertheless seen every year.

The following ten species of helminths have been detected among the ribbon seals of the Bering Sea. Cestodes *Diphyllbothrium* sp. and *Diplogonoporus* sp. have been found in the intestine. Nematodes of Anisakidae gen. sp. have been found in the intestine and stomach; *Contracaecum osculatatum* Rud., detected in many species of Pinnipedia in the Northern and Southern hemispheres, localizes in the intestine (not detected among ribbon seals of the Sea of Okhotsk). *Phocascaris phocae* Höst, known only among harp seals as well as ribbon seals, parasitizes predominantly the stomach.

Terranova decipiens Krabbe was detected only once in the stomach of ribbon seals; it is known among walruses, sea lions, fur seals, elephant seals, and many species of true seals. Another species of this genus, *Terranova azarasi* Yamaguti and Arima, was found in the intestine of ribbon seals from the Sea of Okhotsk but not the seals of the Bering Sea. From among the acanthocephalans, *Bolbosoma nipponicum* Yamaguti was also found among many marine mammals of the Pacific Ocean basin. It localizes in the intestine, as does *Corynosoma strumosum* Rudolphi, known
338 among a large number of species of Pinnipedia and also among some land mammals and birds. *Corynosoma semerme* Forssel, widely distributed among Pinnipedia and cetaceans of the Northern hemisphere, is also found among ribbon seals (Delyamure, 1955; Shustov, 1965c).

Natural mortality of this seal has not been studied. As in other species, mortality is maximum in the younger age groups. Death caused by enemies is evidently insignificant but parasites can cause death, albeit to a small extent. Maximum mortality arises from unfavorable ice conditions and other abiotic factors.

The scattered disposition on drifting ice floes suggests that there is no competition with other species for a place on them. Only at the end of the icy period, in the years of early thawing, when many seals of four species gather on the rapidly diminishing ice massifs, is competition possible between the bearded seal, common seal, ringed seal, and ribbon seal. There is hardly any competition in relation to food since the food zones of all these species are distinctly "delineated".

Population dynamics. The natural population dynamics of this seal have not been studied but its fluctuations cannot be significant. In recent decades this situation has undergone significant changes as a result of hunting. Before hunting with the help of ships was organized (1932), the ribbon seal was caught by the local people in very limited numbers since it essentially stayed far away from the coasts. This level of hunting had hardly any impact on the seal reserves and the population maintained a natural equilibrium. In the first two decades, hunting was carried out only in the Sea of Okhotsk where the comparatively low level of killing did not alter the natural state of the population. As the hunting fleet enlarged in the early 1950s, and the catch of all species of seals increased, some 20,000 ribbon seals were caught annually. An analysis of the age composition of the seals caught revealed a gradual "rejuvenation" of the population but pointed to a disturbance of the natural ratio of the age groups and a reduction in the reproductive capacity of the population. The results of these investigations formed the basis for suggestions regarding the need to restrict the killing of the ribbon seal in the Sea of Okhotsk.

Hunting of the Bering Sea population commenced only in 1961; until then the population had remained undisturbed. An analysis of the hunting activity of ships and the age composition of the animals caught in 1961-1963 showed that the ribbon seals killed per day decreased considerably irrespective of hunting conditions. The specific proportion of the larga, which is the most difficult seal to kill, increased in the catch of the ships; larga becomes the target only when seals of other species are not available. The age composition of the catch also changed. In 1961, the average age of the ribbon seals caught was 9.8 years; it fell to 6.9 years in 1962, and further dropped to 4.9 years in 1963. This points to a reduction of the total population and its reproductive capacity since females older than five years are the most productive (Shustov, 1965).

With expanded hunting in subsequent years for newborn pups because of their valuable fur, the age composition of the animals killed somewhat balanced but the state of the population still causes anxiety.

Field characteristics. Characteristic coloration is an unfailing feature for recognizing the ribbon seal (Fig. 184). The seals are found only on white, clean, and stable ice floes drifting far away from the coasts; they do not form groups and are usually seen singly or in twos and threes. In the summer months these seals adopt a pelagic mode of life; sites of summer gatherings have not been established. (V.A.)

339

Economic Importance

The ribbon seal is of little importance to the local people who hunt in the coastal zone where its population is very small. The proportion of the ribbon seal in the ship catches in the Far East is not less than 30% of the total catch (over 80% in the Bering Sea) and thus its importance here is quite substantial. It should be borne in mind that the ringed seal, which represents the largest number of seals caught, is a much smaller animal and provides a smaller quantity of useful products compared to the ribbon seal.



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Fig. 184. Adult male ribbon seal on an ice floe. Bering Sea (photograph by A.P. Shustov).

Seals of all the species are killed in the Far East using firearms from motor boats dropped in the water from a schooner in the hunting region. Seals resting on ice floes represent the predominant target since killing the animals in the water inevitably results in great losses as most of these killed in the icy period drown.

The products of hunting are the hide, fat recovered from the subcutaneous blubber, and the carcass. The blubber is removed at the site of the kill (on the ice floe). Its further processing is carried out either on some suitably equipped ship or at the coastal base where the ships deliver the raw products for processing. Salt is used as a temporary preservative of raw skins on the ships. The hides of adult seals are mostly used as raw leather while those of white pups and the better quality skins of adult animals serve as valuable raw material for the fur industry. The fat recovered is used for commercial purposes in tanning, metal, and other industries. The carcass is a valuable product for the animal breeding farms extensively organized in the Far East; the meat and bones are used as feed for fur animals. The local population fully utilizes the animals killed.

340 Both the populations of the ribbon seal are exposed to heavy hunting (see "Population Dynamics"). The results of investigations indicate the need for an extremely careful approach to utilizing these populations. Hunting norms should be fixed annually for each population on a rational basis depending on its condition and strict adherence to the norms enforced. (V.A.)

Genus of Gray Seals

Genus *Halichoerus* Nilsson, 1820

1820. *Halichoerus*. Nilsson. Skand. Fauna. Dägg. Djur., I, p. 376. *Halichoerus griseus* Nilsson = *Phoca grypus* Fabricius.

These are relatively large seals, the adults measuring about 2 m or more (*Lc*). The facial portion of the head is noticeably elongated (more than twice the distance from the eyes to the ear opening) and elevated. Its height in front is almost the same as at any other point while the upper contour of the profile draws an even or slightly convex line at the bridge of the nose. The whiskers are flattened, with wavy edges. The first and the second digits on the fore flippers are longer than the others.

The profile of the skull is seen as an almost perfect straight upper contour from the occipital crests to the anterior margin of the nasal bones; the height of the facial portion on the anterior margin of the nasal bones is no less than the height of the cranium.

The anterior nasal opening is extremely elongated and opens upward; the maximum width occurs in its posterior one-fourth. The nasal bones are relatively short (not more than one-fifth the condylobasal length) and broad; their total width at the anterior margin is about one-half or more their length. On the posterior (orbital) side of the zygomatic processes of the maxillary bones lies a horizontal carinate crest which conceals the suborbital aperture when viewed from above. The length of the zygomatic bones without process is more than double their smallest width; the lower posterior process of these bones is considerably longer than the upper. The features of the tympanic bullae, viewed from below, appear as a triangle with rounded apices and resemble those in seals of the subgenus *Phoca* s. str. The bony lobe of the external auditory meatus is simple in design, flattened and broad.

The premolars and molars, except for the first molar, are massive; the second and third premolars and molars of the upper jaw and also the first three premolars of the lower jaw have conical crowns and lack accessory cusps; accessory cusps are seen on the fourth premolar of the upper and lower jaws and on the lower molars; highly reduced accessory cusps are sometimes seen even on the initial premolars. A second molar is sometimes seen in the upper jaw. At least the three initial premolars of the upper and lower jaws among adults have a single root. True molars, however, invariably have two isolated roots set in separate alveoli. Incisors have laterally flattened roots. The dental formula is:

$$I \frac{3}{2}, C \frac{1}{1}, P \frac{4}{4}, M \frac{1}{1} = 34 \text{ or } M \frac{2}{1} = 36.$$

The neonatal pelage is white with a creamy tone; after the first molt the hair coat is spotted.

The females are somewhat smaller than the males.

There is one pair of teats.

Ecologically, the genus is represented by two forms. One form inhabits the Baltic Sea and also partly the Canadian-Newfoundland waters and is biologically associated with ice floes. These seals reproduce, suckle the pups, and molt on ice floes. The herd instinct and polygamy are less characteristic of this form. The population of the second form, inhabiting unfrozen waters, exhibits no affinity for ice floes, spends part of the time on the coasts, and forms rookeries of a distinct harem type. Whelping, lactation, and partly even molt occur on the coast.

The distribution of the genus is restricted to the coastal waters of the boreal belt of the North Atlantic and is now mainly confined to three isolated portions of this belt: western Atlantic (American), eastern Atlantic, and Baltic. The American section is bound by waters from the southern boundary of the Gulf of Maine almost up to northern

Labrador, including the Gulf of St. Lawrence and Newfoundland coasts. The European section comprises the waters surrounding Iceland, the Faeroe Islands, Ireland, and Great Britain, and also the coastal waters from Bretagne and La Mancha to eastern Murman, including the North and Baltic seas, and also the inlet zone of the White Sea. The boundaries of distribution are mainly determined by the lines of the polar front and heavy pack ice, continental shelf zone, and boundaries of the temperate boreal waters. The distribution as a whole is characterized by interruptions, being broken into fairly distinct isolated sections. Thus one of these, the Baltic, is isolated from the eastern Atlantic which, in turn, is wholly isolated from the western Atlantic.

The origin of the genus has been traced to the Pliocene as genus *Gryphoca* van Bened. Deeper roots of the genus have not been detected. It is possible that the Miocene seal, *Miophoca vetusa* Zapfe, represents only one of the much older ancestral branches of this phylogenetic group.

These seals exhibit the most proximate contemporary genetic associations with seals of the genus *Phoca* (especially of subgenera *Phoca* s. str. and *Pusa*) together with which they form the subtribe Phocina (Chapksii, 1955).

The genus consists of a single species, the gray seal or "tevyak," *Halichoerus grypus* Fabricius, 1791, which constitutes 5.5% of the number of species in the family. There is no basis for assuming that the genus consisted of a larger number of species in the geological past. The economic importance of gray seals is not significant.

The USSR is host to this single species, or 7.7% of the number of pinnipeds in our fauna and 0.3% of the number of species in our mammalian fauna. Its distribution is restricted to the Baltic Sea and southwestern part of the Barents Sea. The economic importance of the genus in our waters is altogether negligible. At places, some probably damage the fish reserves by consuming particularly valuable fishes, i.e., salmon and eels. (K.Ch.)

GRAY SEAL¹¹⁸

Halichoerus grypus (Fabricius, 1791)

1791. *Phoca grypus*. Fabricius. *Scrivter of Naturhist.-Selskabet*, Kjobenhavn 1, p. 167, pl. 13. Greenland.

¹¹⁸ "Tevyak" is a name used by the coastal people but is not less common. Known as "zhirovets" at places in Murman. Other names—"long-snouted," "gray," "hump-nosed," "pig," and other artificial, bookish, often translated names—are almost out of use since the coastal inhabitants are little acquainted with these names or this species.

1820. *Halichoerus griseus*. Nilsson. Scand. Fauna, Dägg. Djur., I, p. 377. Greenland.
1851. *Halichoerus macrorhynchus*. Hornschuh et Schilling. Arch. Naturgesch., 17, p. 28: Baltic Sea.
1851. *Halichoerus pachyrhynchus*. Hornschuh et Schilling. *Ibid.* Baltic Sea.
1886. *Halichoerus grypus* var. *atlantica*. Nehring. Sitz.-Ber. Ges. Naturforsch. Freunde, Berlin, p. 122. Western coast of Norway.
1886. *Halichoerus grypus* var. *baltica*. Nehring. *Ibid.* Baltic Sea. (V.H.)

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Diagnosis

Only species of the genus.

Description

General build of body massive, without distinctive features, while preserving all the typical features of the subfamily of true seals (Fig. 185). However, the snout is elongated, high; the profile at the eye level shows no curvature. Some skin folds¹¹⁹ are seen posterior to the ear opening. The whiskers are set in six rows on the upper lip; the first to the third rows from below have 7-9 each. On the fore flippers, the first digit is the longest (with the claw), the second slightly shorter, while the length of the others decreases markedly toward the last.

The color of the hair coat reveals considerable individual variation depending on age and sex and, further, is subject to some geographic variation. The coloration essentially consists of two elements: the general background and the fairly dark spots dispersed on it. The background and partly the spots exhibit a wide range of gray tones and shades, from extremely light silvery-white to, at places, almost white to very dark, and even totally black. The main background in most cases is considerably lighter than the spots and is usually different on the dorsal and ventral
343 sides, the latter almost invariably being perceptibly lighter. The spots are of diverse sizes and shapes; the sharpness of their contours, number, and disposition also vary. From very early times, many authors (Millais, 1904; Collett, 1911-1912; Ognev, 1935; and others) attempted to group all the

¹¹⁹ This formation was described by Pocock (1933) who regarded it as a rudiment of the outer ear shell. However, these skin prominences, measuring 3 to 15 mm (Mohr, 1952), cannot be regarded as typical of the species. There is even less justification to view them as analogous to the rudiments of outer ear shells. These skin folds are altogether lacking in the Baltic gray seals.

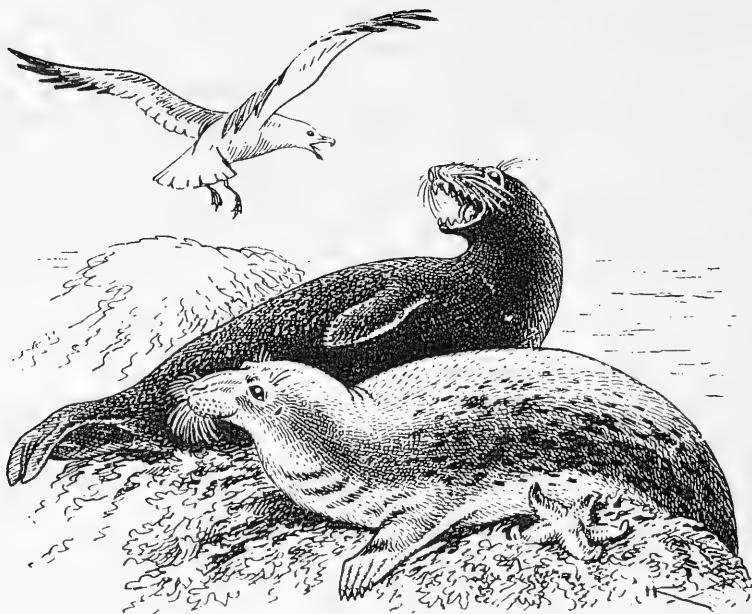


Fig. 185. Gray seal ("tevyak"), *Halichoerus grypus* (figure by N.N. Kondakov).

diverse colors into two main types. One type covered animals with a relatively lighter, contrasting spotted coloration and the other type animals with a much darker, dull-spotted coloration. According to this scheme, the light gray main background on the dorsal side of animals with light coloration is somewhat darker and covered with innumerable, predominantly dark gray, blackish spots, sometimes scattered singly though quite densely and sometimes gathered in clusters which are often fused. Some spots have distinct contours while others are quite diffuse. The angular, sometimes complexly contoured spots on the sides of the neck, on the chest, and on the shoulder blades exhibit the utmost contrast. The spots at these sites are also the most vividly pigmented, at places almost pure black. On the dorsal side, the spots are duller and generally lack sharp outlines.

The dark-colored type animals are distinguished by a very dark general shade that depends not only on the darkening of the main background, but also on the intensity of pigmentation of the spots covering it and the increased number of spots or their sizes. Concurrently, the contrast of the pattern either disappears or weakens due to the indistinct, diffuse contours of the spots. When the background is particularly

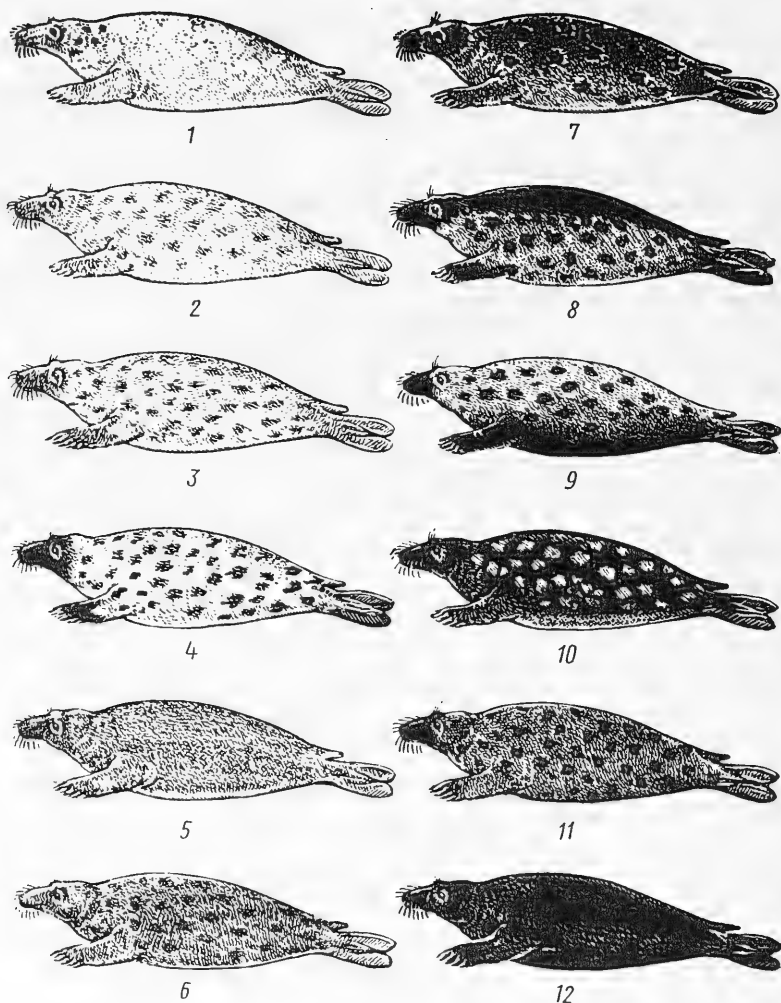
darkened and the spots are fused, the animals appear from a distance to be monochromatically dark-colored, almost black. On closer examination, the spots are definitely apparent; furthermore, small, sparsely scattered, light-colored specks are discernible on the dark skin, either in streaks or blotches.

Various transitional coloration forms are noticed between these two extreme types. The following features are characteristic of males as well as females among all the diverse types. The dorsal side is gray or bluish-gray, with fairly innumerable almost black spots; the underside of the body is almost white with highly contrasting black spots that are particularly prominent in the anterior portion of the body.

In spite of the extensive studies on the color variation of this species, its earlier descriptions (Millais, 1904, and authors citing Millais; Ognev, 1935; and others) are no longer adequate, i.e., attempts to differentiate two main color types—light- and dark-colored animals, or at least the greater number of them. The information collected in the last two decades has provided data pertinent to the prevailing situation. There is no doubt about the existence of predominant color types but these can now be more conclusively interpreted as individual, age-related, sex-related, and evidently geographic variations. The magnitude of this variation differs in different population groups. Evidently, its range is most extensive among the land-loving (pagophobic) gray seals inhabiting the European and American Atlantic. The Pagophilic Baltic seals are evidently characterized by a relatively greater color stability.

Only the Murman gray seal can be regarded as a representative of the Atlantic population in our waters. Its color is very similar to that of the British-Irish populations and is perhaps indistinguishable from the color of the latter. It is characterized by as much range in individual variation as in the first year after the initial neonatal molt (Fig. 186). Among such molted pups, the color intensity of the main background as well as the nature of spots (size, shape, and sharpness) and the intensity of their color vary; the color may be very light or sometimes very dark "on any general background". Wholly monochromatic black-colored animals are also encountered (Karpovich, Kokhanov and Tatarinkova, 1967). A similar color variation is seen among the juveniles of British-Irish and
 344 Norwegian populations. In these regions pups are encountered with and without spots, with a bluish-gray main background, even greenish, sometimes creamy-white or dark-colored or pure black; some animals are brownish or even reddish-brown (Millais, 1904; Collett, 1911-1912).

Color variation among the adults is even more diverse. At times, it is difficult to find two animals with totally identical coloration. Nevertheless, the color of Murman gray seals does not go beyond the various



344 Fig. 186. Individual color variation of molted juvenile gray seal, *Halichoerus grypus*. Great Ainov Island, Murman coast (after figures by V.D. Kokhanov).

shades of gray and varies from almost white to almost or even totally black. This is true of the main background on which the spots are dispersed and of the spots themselves. The main background is more often of light gray shades, sometimes whitish and at places almost totally white; specimens with a very dark, almost black background are not very rare.

345 On the underside of the body, the background color is somewhat lighter

than on the upper side, but this difference can sometimes be evened out by the significantly greater spottiness on the throat, chest, and belly, compared to the dorsal side on which the spots are frequently duller.

The spots vary widely in shape, size, sharpness, color intensity, and density. In most cases the spots are diverse, often of queer shapes and extremely dissimilar in size even in the same animal. The larger spots have sharp as well as highly diffuse contours. The spots on the flanks and underside of the body are the most intensely pigmented and contrasting; they are often totally black. The spots are usually 10 - 15 cm in size; innumerable much smaller spots, down to mere specks or dabs, are scattered between very large ones as well as separately from them, descending onto the throat, occiput, and the base of the fore flippers. Extremely matte and comparatively small spots sharply predominate on the dorsal side. Thus the entire dorsal surface very often appears from a distance light-colored and monochromatic. At the same time, animals are encountered with totally dark or black coloration, this being characteristic of males. The main background as well as the spots never contain admixtures of brown, cinnamon, rust, or yellow shades but these are encountered, albeit very rarely, among the animals in British rookeries.¹²⁰

A very similar sharply manifest sexual dimorphism points to the genetic kinship of the Murman gray seals with the other gray seals of the open Atlantic waters breeding on the land. Adult males are distinguished from females by a very dark and fairly monochromatic color. Males are not characterized by contrasting spots and their body underside is only slightly in color than the upper side. On the contrary, brighter coloration is characteristic of the females, among which the main background is much lighter, especially on the flanks and ventral side, where it is very light. The spots on this background are highly contrasting but vary in degree of sharpness of contour, which is sometimes well defined and sometimes highly diffuse. These spots are concentrated predominantly on the front portion of the body where even contrasting specks stand out.¹²¹

The age-related color variation among the pagophobic and pagophilic forms has not been thoroughly studied. Evidently, in the early stages of postnatal growth, their color differs only as much as the groups under comparison differ in the range of individual variation. Pups of

¹²⁰ The above color characteristics of the Murman gray seal are largely based on the reports of V.D. Kokhanov, a zoologist in the Kandalaksh sanctuary.

¹²¹ The contrasting fanciful patterns of bright black coloration of the Murman gray seals renders them visible from a distance even in twilight hours. Thus, several tens of animals lolling on the coast appear "surprisingly similar to a herd of spotted cows at rest. Their white skins appear variegated with large and small black spots" (Belopol'skii, 1951).

different ecological groups form herds of unmolted white pups. In most of the pups of the Atlantic population, the short hair coat after the long embryonal hair has been shed is almost the same as among the pups of the Baltic seals. Its typical features are as follows: The main background is pale gray, usually somewhat darker on the dorsal surface than on the ventral. Comparatively small but numerous dark gray or even olive-colored spots, often fused, are scattered fairly uniformly on the upper as well as the underside of the body. The sharpness of the spot edges varies in different sections of the body of even the same animal as also in different animals; in the anterior portion of the body, however, and in particular on the flanks, chest, and neck, the spots mainly have sharp outlines and hence stand out contrastingly. Such a coat among the juveniles usually appears brighter and somewhat "fresher" than among the older seals.

346 The molted pups of Murman reveal up to 12 distinct color variations which can be grouped into the following six classes: (1) almost black, monochromatic; (2) dark gray, with very dark spots only on the trunk; (3) similarly dark gray but with spots on the head as well as on the flippers; (4) close to black, with light-colored spots; (5) with light gray main background and dark, almost black snout and extremities of fore and hind flippers; and (6) with the same light-colored background and slightly darker colored head, flippers, and spots of the same shade scattered on the trunk (V.N. Karpovich, V.D. Kokhanov, I.P. Tatarinkova).

The pups from the Baltic Sea after shedding the embryonic pelage appear more monotypical. They are then gray with innumerable blackish, partly fusing small spots. Instances of black or almost black coloration have not been seen among these pups. The spottiness covers the entire head and extends to the occipital, temporal, and throat regions (Lilljeborg, 1874; Allen, 1880; Schubart, 1929; Lönnberg, 1929; Freund, 1933; Mohr, 1955; and others).

The subsequent color changes of the hair coat until the animal attains maturity have not been adequately understood. Some authors (Collett, 1881; Millais, 1904; Mohr, 1955; and others) believe that the original vivid and contrasting spots (with sharp contours) are gradually lost as the animals grow up, giving place ultimately to a uniformly gray or very dark coloration. But this is not actually so. There is no single pattern of age-related color variation that can be regarded as common to all the animals or to different populations. This is indirectly supported by the considerable diversity of the original coloration of the pups, especially the specimens that are found to be almost black from the moment of casting the embryonic pelage. Although there is no possibility of their turning blacker later, even these pups change color. Thus, one gray seal

that lived for several years in the basin of the Bergen Biological Station was almost black with a brown tinge at the age of one month; it began to lighten in color after two years (especially the main background between the spots) and roughly ten years later again turned very dark (Collett, 1911-1912). Observations of two juveniles sporting different colors in the Berlin Zoological Garden showed that the hair coat of the light-colored animal became even lighter and spottier after each molt, while that of the dark-colored animal, on the contrary, became darker so that the spots became increasingly less distinguishable (Nehring, 1887).

Whatever the pattern, the pup at the transitional age is characterized mainly by a transitional color with larger, more contrasting spots than pups that have not yet attained the final pattern (or color type) characteristic of the adults of the corresponding sex. Evidently the young animals do possess some features reflecting their affinity to one or the other ecological groups: Atlantic or Baltic. The growing juvenile from the Baltic Sea is apparently characterized by a gradual loss of the contrast of spots from year to year; the spots either become less distinguishable on the generally darkened background (Ropelevskii, 1952), or they disappear altogether (Mohr, 1965), or become diffuse or sparser. Among the males in general, the spots are lost sometimes in a wholly dark background (Aul, Ling and Paaver, 1957). The spots are less sharp among young animals of transitional age and among the Canadian population (Mansfield, 1963). On the other hand, the view has been expressed that the color and spottiness of at least part of the British-Irish gray seals are as diverse among young animals as among adults (Millais, 1904). On the whole, a clear picture of the age-related succession of color changes among the various populations is not yet possible.

347 The process of color variation in the much later stages of age proceeds divergently, i.e., begins to show sex-related differences. Concomitantly, changes in the configuration of the spots characteristic of the males and females continue and many spots enlarge and lose their sharpness of contour.

The color of the adult males of the Baltic seals is generally quite uniform and falls in the category of spotted coloration described above, being only somewhat duller. The main background of the dorsal side of the body is Smoky-ash with dove-olive tones. It is noticeably darker on the flanks and on the ventral side and the boundary of the background color is often quite distinct. Innumerable dark-colored spots are scattered all over this general background. On the dorsal surface, they are mostly small with diffuse outlines that are generally regular (less often, highly sinuous) and not very contrasting. On the flanks and ventral side the spots are denser, appear very dark (black), often fuse with

each other, acquire very complex outlines, and stand in sharp contrast against the light-colored background. The spots are noticeably larger in the anterior half of the body than in the posterior half; the spottiness on the belly is paler and quite often looks like marble streaks. The spots become smaller around the head and on the throat and look like dabs. Fine specks are sometimes seen even on the occiput, sometimes extending also onto the snout; on the sides of the head, near the eyes and ears, however, the spot-dabs are as numerous as on the throat. The snout and the upper portion of the head are also quite often monochromatic, grayish dove-colored. Quite often, too, fine specks descend even onto the fore flippers. On the lower side of the neck and on the chest, the spots form a typical pattern, more often a longitudinally elongated garland of fused dark gray spots with diffuse contours standing out sharply on a very light-colored background. On the belly the spots are not only paler, but their outlines more diffuse.

Adult female Baltic seals, compared with males, are generally lighter in color and less spotted (Aul, Ling and Paaver, 1957). It is possible that the spot pattern on the neck and chest is better developed among females than males (brighter and more contrasting).

The hair coat fades somewhat in the course of the year. Among the British-Irish and Norwegian populations, the skin turns very pale by spring and the spots lighten; they turn a vague brown on the dorsal surface while the main background between them fades to a monochromatic straw color (Millais, 1904; Collett, 1911-1912).

Sex-related color differences are quite sharp among the Murman gray seals. Adult males are usually dark, almost black, with spots that appear indistinct from a distance. Only the underside of the body is lighter with dark spots being fairly distinct. The females are lighter and more spotted than the males although dark females do occur occasionally (V.D. Kokhanov). Seven basic color variations have been recognized among the females. The males and females exhibit deviations (roughly 12%) wherein the males exhibit the color features characteristic of females and vice versa. Sex-related color differences are seen among Murman gray seals right from the earliest age, i.e., as soon as the pup begins to shed the original (embryonic) pelage.

The main body background in most young females is light gray with scattered darker gray spots. Less frequently, the spots are black on a light gray or even darker background. A very dark, almost black main background (lighter on the underside) predominates among the males; in the first case the scattered spots are black and in the second light colored (lighter than the main background) (V.D. Kokhanov, V.N. Karpovich, I.P. Tatarinkova).

Sex-related color changes are also similar among the Norwegian (Collett, 1911-1912) and British-Irish (Hewer and Backhouse, 1959) populations of gray seals. This confirms the greater affinity of the Murman gray seals with the European-Atlantic population than with the Baltic. The adult males of the Norwegian population are dark-colored, almost totally monochromatic blackish-brown; the lighter-colored animals show a dark gray main background alternating with large brownish-black spots. The females are lighter in color: the main background is either brownish-gray or silvery-white as in the juveniles and the spots sometimes more, sometimes less vivid; sometimes spots occur only on the shoulders; some animals are totally devoid of spots and appear fairly monochromatically white from afar; the spots vary from light brown to very dark (Collett, 1911-1912).

The sex-related color differences of the hair coat are similar among the British-Irish populations. The main background in adult males is a uniform dark color interrupted quite often by not very contrasting and rather small clearances in the form of angular white spots and motleys, sometimes with complicated patterns. In females, innumerable dark spots are scattered on a very light-colored main background (usually differing in vividness on the dorsal and ventral sides). These spots are invariably darker than the main background and the contrast is quite good in most females. Among the dark-colored males, the main background is close to black with indistinct small and narrow white streaks showing through. Among the dark-colored females, the main background is dark gray and the spots are numerous, quite large, and deeply pigmented, almost black. Light-colored males are distinguished by a very pale, brownish-gray main background covered with very bright, sometimes almost white streaks. Light-colored females have a light gray main background covered with comparatively sparse and small spots (Hewer and Backhouse, 1959).

Coloration is also similar among the Canadian gray seals. The males sport a dark gray, almost black, background color patterned with tiny dark gray spots on the flanks which may fuse into large groups. The overall impression is a very dark coloration. The color of the females is smoky-gray dorsally, turning silvery-gray or even white along the flanks and on the belly. In much older animals, the dark gray or black spots may have fused. The female in general is lighter in color and more spotted than the male (Mansfield, 1963).

Among the females in the British section of the range, stray specimens are encountered, albeit very rarely, with an orange-rust-red head, neck, and lower surfaces of the flippers, and sometimes rust-colored flanks; elsewhere the body color remains normal (Backhouse and Hewer,

1957, 1960). Animals with this type of coloration have not been reported in our waters and it has been emphasized that even brown shades are not found among the Murman gray seals (V.D. Kokhanov).

The skull is massive, the facial portion appears elongated, and the rostral portion broad (Fig. 187). Among adults the width between the zygomatic bones noticeably exceeds that of the skull between the mastoid processes; the maximum lateral bulge of the zygomas falls close to the posterior margin of the orbit, in the posterior half of the skull. The interorbital space is moderately compressed (its width is not less than 15 mm among the adults).

The general appearance of the skull resembles more that of a large large or Atlantic common seal but differs in the structure of the anterior nasal opening, nasal bones, massive rostral portion, nature of crests, form of the lower jaw, and especially the sharp structure of the crowns of the premolars. The broad and short nasal bones have a shortened apex, forming more than half a right angle, with rectilinear sides. The anterior margin of the nasal bones has three deeply incised denticles. The nasal processes of the pre-maxillary bones reach the nasal bones but only adjoin them (not invariably though) and do not wedge deeply between them and the upper maxillary bones. The longitudinal bony septum in the choanae falls far short of the posterior edge of the bony palate incised in the form of a deep arc. The anterior palatine openings are large, with a deep troughlike pit anterior to each. The width of the tympanic bullae together with the bony lobe of the external auditory meatus exceeds their length. The sagittal crest is straight, narrow, and relatively low.

349 Most of the premolars and the upper molars have a high conical crown, without accessory cusps. The latter are developed, though not intensely, only on four premolars and lower molars (and often also on the lower initial premolars). These are in the form of small denticles disposed one each anterior and posterior to the main cusp at its base. Intensely reduced and barely visible denticles are seen even on some other premolars at the base of the crowns. The canines are relatively large (the longitudinal diameter of the alveolus is more than 10 mm); the extreme lateral incisors in the upper jaw are somewhat larger than the rest.

Individual skull variations are significant in terms of absolute units as well as ratios. The structure of the crown of premolars is variable. Sex-related differences in the skull are manifest only in sizes and some ratios; the skull of males is larger.

Age-related skull variations are seen primarily in the elongation of the skull due to the predominant growth of the facial portion which becomes more massive and increases in height. Among young animals, the facial portion falls much below the occipital and the line of the upper

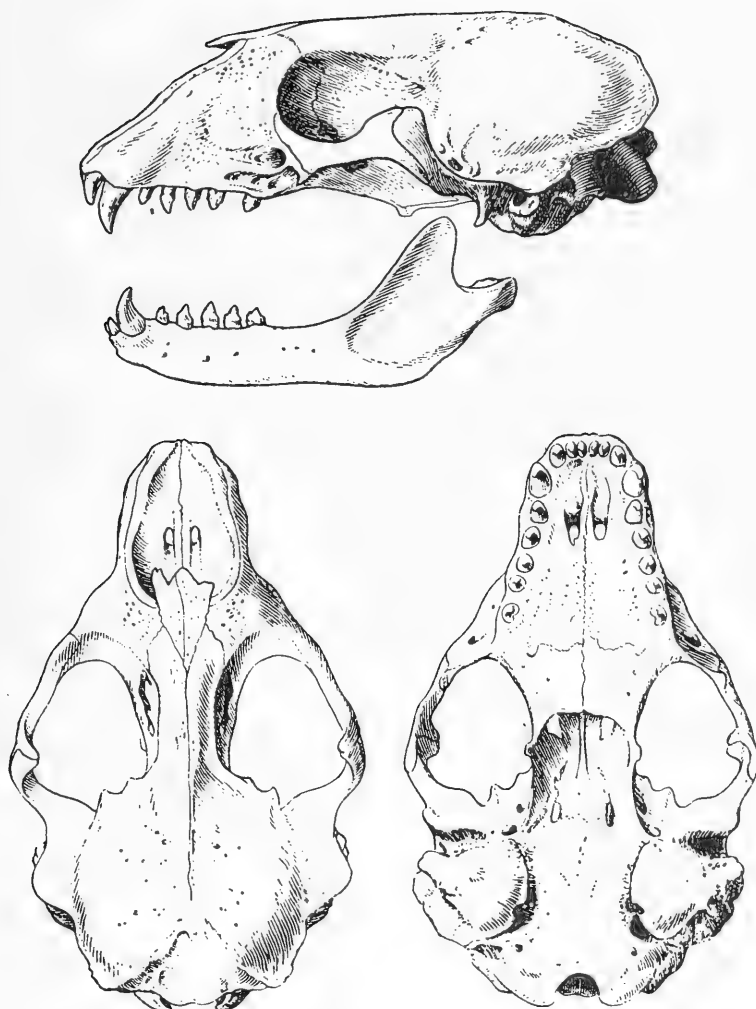


Fig. 187. Skull of the gray seal, *Halichoerus grypus* (figure by N.N. Kondakov).

profile of the skull is intensely inclined toward the anterior margin of the nasal bones. The width at the zygomatic arches is less developed among young animals than adults; it does not exceed the width at the mastoids in the young; the width of the rostrum at the level of the upper canines too is relatively smaller than in adults. The contour elements of the cranium (crests) are almost undeveloped among young animals. The sagittal crest is not manifest: instead, only folds are seen to the right and left of the median. These folds slightly diverge sideways and form a small elongated area; occipital crests, seen as cornices in adults, are

practically absent in the young. As in other seals, the roots of the teeth are initially hollow and thin-walled but intensely thicken over time and the pulp cavity fills in. Among many old seals, the roots are unusually hypertrophied due to the cement layers while the crowns are worn down almost to the base. Over time, all the skull bones thicken, as a result of which the overall weight of the skull also increases.

The individual and partly the geographic variation of body size is significant; females are generally smaller than males. The body length of the adults measured from tip of nose to tip of tail along the dorsal surface (*Lc*) varies from 170-250 cm. This length in the largest animals can reach 3 m. However, various authors cite different values: 2-2.5 m (Freund, 1933), 2.5-3 m and at places where these seals are killed most intensely (southern Baltic), mostly 2-2.5 m (Mohr, 1952). According to the old data (Lilljeborg, 1874), the body length of the Baltic male gray seals is 195 cm and that of females 175 cm.

Data on the body length of male Murman gray seals are extremely limited and not wholly reliable. According to some authors, the average size of an adult animal is 2.5-3 m (Skvortsov, 1928*) and according others (Belopol'skii, 1951), the males are 2.5 m long. A large male caught on Franz Josef Land measured 263 cm along the dorsal surface (*Lc*) (Tsalkin, 1936).

The body length of gray seals of the British and Irish populations (from which the size of Murman gray seals can be judged to some extent) varies from 245 to 260 cm in males (largest male measured 292.5 cm) and 168 to 198 cm in females (Millais, 1904). The average length of adult Canadian male gray seals is 235 cm, of females 200 cm (Mansfield, 1963). The available information on weight is also in general terms. It ranges from 130 to 320 kg for seals of both sexes. During lactation, the females lose over 30 kg of weight and males in the mating period even more than 50 kg (Collett, 1911-1912).

The condylobasal length of the skull is 240-270 mm and its maximum length [?] 330 mm (Collett, 1911-1912). This length among females is considerably less than among males: 264 mm in the Baltic male seals and 240 mm in females (Lilljeborg, 1874). In the largest males of the Atlantic region, it reaches 320 mm (Allen, 1880) and even 330 mm (Collett, 1911-1912) while it hardly exceeds 260 mm in the largest of the females. The width of the skull at the zygomatic arches reaches 200 mm. (K. Ch.)

Taxonomy

Only species of the genus.

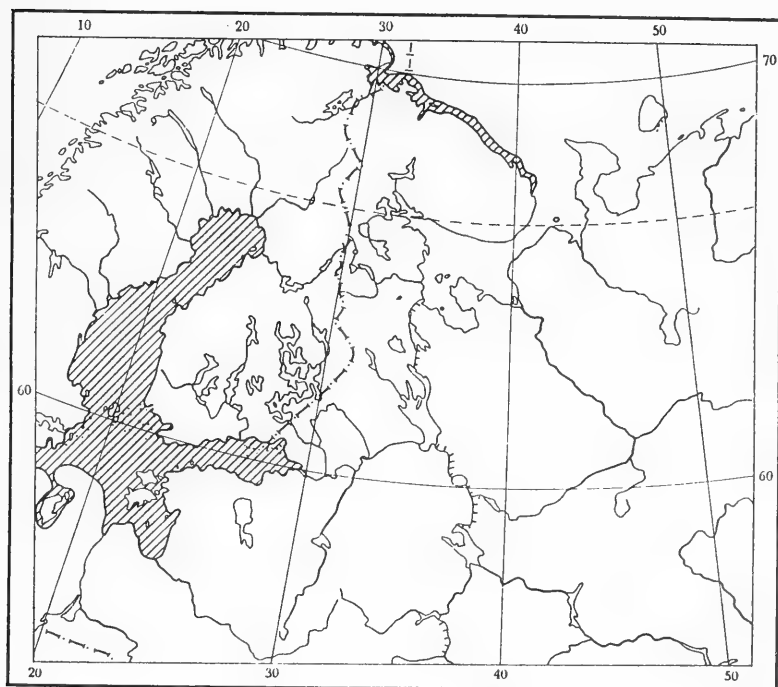
Geographic Distribution

Temperate latitudes, partly the cold belt of the North Atlantic from Canada and the adjoining regions of the USA to the coasts of central and Northern Europe and the Baltic Sea. The range is broken into fairly isolated sections.

Geographic Range in the USSR (Fig. 188)

This covers the easternmost part of the world distribution and includes two distinct regions: coastal waters of Murman and the Baltic Sea.

351 The gray seal is distributed all along the coastal belt of Murman from Varanger Fjord to St. Nos Strait and possibly farther in the southeast up to the western threshold of the neck of the White Sea. However, the find of the gray seal on the eastern extremity of the range is evidently sporadic and it is only very rarely that this seal is found in the neck region itself (Schrenk, 1955*; N.A. Smirnov, 1929; Kirpichnikov, 1932). Details of the seal distribution and the disposition of all of its coastal



351 Fig. 188. Distribution of gray seal, *Halichoerus grypus* in the USSR (K.K. Chapskii).

rookeries have not yet been established. The gray seal reproduces for certain or resides regularly on the Bolshoi (Large) and Malyi (Little) Litskie, Veshnyak, Kuvshin, Malyi Zelenets, Kharlovskie ("baklyshes"), Semioistrovnye ("ludy"), Ainov and other islands, and in the region of Dal'nii Zelenets, Iokan'gi, Teriberki, and Pala Bay. The gray seal whelps presumably in the bays of Rakushnaya, Voyak, Fedotovsk, and Korabel'naya (Karpovich, Kokhanov and Tatarinkova, 1967).¹²²

The view that the eastern boundary of distribution extends up to Novaya Zemlya, based on the record of this seal by K. Ber on the west coast of Novaya Zemlya, is erroneous. This is an exceptionally rare event of the straying of an animal far beyond the range of its distribution. Very similarly, a lone gray seal was also caught in Franz Josef Land archipelago (Tsalkin, 1956*). The same is the situation with regard to the White Sea, which was included in the distribution of this species (Schrenk, 1855*), although episodic finds of lone animals have been reported from eastern
 352 Murman in the inlet region and the adjoining neck regions (N. Smirnov, 1929; Kirpichnikov, 1932; A.G. Beloborodov; and others). It is quite likely that lone animals even more rarely can penetrate into the northern part of the neck region too.

In our Baltic waters the gray seal is encountered from time to time in the northern coastal belt of the Gulf of Finland from the boundary with Finland to Nevsk Bay, while it is quite common in the southern coastal zone commencing from Kopor Bay and farther west. It is encountered on the Estonian coasts all along the Gulf of Finland but is mainly confined to regions far removed from the mainland coast, with a preference for the tiny islets scattered there (Aul, Ling and Paaver, 1957). It inhabits Irben Strait and the Gulf of Riga (its Estonian as well as Latvian sections) including Rukhnu Island. Evidently, from time to time, especially in water, it is seen in the Latvian marine coastal waters. Rare encounters in the coastal belt of the sea within Lithuania and Kaliningrad districts are possible since gray seals were found in the past on the coasts of the former eastern Prussia, Pomerania and Ryugen Island, as also on the coasts of the former Polish corridor.

¹²² The first reference to the distribution of the gray seal beyond the Polar Circle in our territory was made by I. Lepekhin (1805). Concrete evidence of the catch of gray seal in Varanger Fjord (Pleske, 1887), on the coasts of eastern Murman (N. Smirnov, 1903), and on Litskie Island (Telegraph of Murman Research and Hunting Expedition, 1906) became available much later. It took an even longer time for more detailed information to become available (Skvortsov, 1928*; Sdobnikov, 1933*; Belopol'skii, 1941, 1951; V. Uspenskii, 1941*). New data have been collected in recent years by the workers of the Kandalaksh Sanctuary.

Geographic Range outside the USSR (Fig. 189)

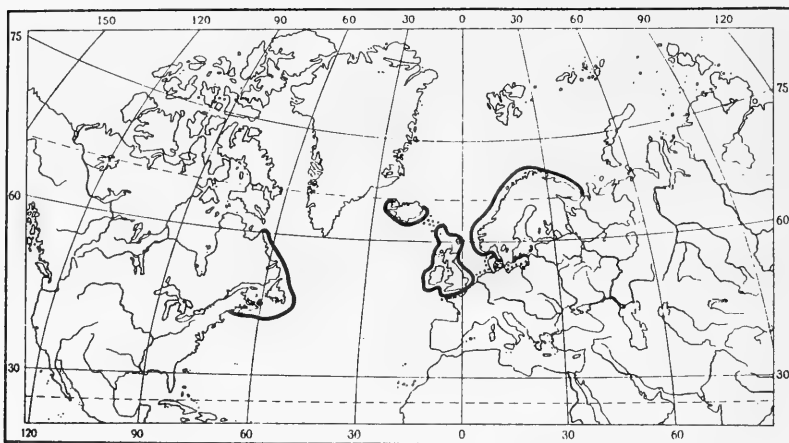
In the Baltic Sea, the range covers the Finland portion of the Gulf of Finland, Gulf of Bothnia, northern and partly central regions of the Baltic Sea itself (from the west, its Swedish belt). To the south of Gotland Island, it is encountered more rarely, in the south up to Eresunn Strait; it is rare in the southern and southwestern parts of the sea, including the coastal waters of the Polish People's Republic, the German Democratic Republic, on the adjoining coasts of Denmark, and the Federal Republic of Germany where it is encountered sporadically. The gray seal is evidently even more rare now in Denmark Strait although the breeding of this seal in the past on Anholt Island in Kattegat has been recorded.

Outside the Baltic Sea, the population in the eastern Atlantic section is concentrated mainly in three regions where the seals breed and reside permanently: 1) region of Great Britain and Ireland including the Hebrides, Orkney, Shetland, and Faeroe islands; 2) coastal waters of Iceland (excluding evidently the northeastern section); and 3) Norwegian coast, predominantly its middle portion where the most important (though not many) breeding sites are concentrated. In general, however, the boundaries of distribution in the European part include the coastal mainland from Bretagne (sporadic), La Mancha, Pa-de-Kal along the southern coast of the North Sea up to the Jutland Peninsula, joining
 353 there with the Baltic and Norwegian sections of distribution extending up to Nordkapp. The presence of this species on the coasts of Spitsbergen is rather doubtful in spite of positive references to it (Saemundsson, 1939).

There are no settled populations on the coasts of Greenland but stray animals and probably even small groups wander there from time to time (Brown, 1868; Allen, 1880; Winge, 1902; and others). The American part of the distribution includes the Gulf of St. Lawrence and the adjoining regions of open coastal waters in the north from the Strait of Belle Isle along Labrador roughly up to the latitude of Hebron (about 68.5° N lat.) and in the south partly along the west coast of Newfoundland, to the south and southwest of this island and Cabot Strait, including Sable Island, coastal waters of Nova Scotia, Gulf of Maine, and up to Cape Cod inclusive. (K.Ch.)

Geographic Variation

The geographic variation of the gray seal has not been adequately studied. Nonetheless, the species distribution is quite fragmented into distinct



352 Fig. 189. Species distribution of the gray seal, *Halichoerus grypus* (K.K. Chapskii).

sections with extremely incomplete contacts between them. First of all, the western Atlantic (American) zone of habitat of the species is practically isolated from the eastern Atlantic (European) zone since gray seals do not reside regularly in the waters of southern Greenland and are sighted rarely and irregularly.

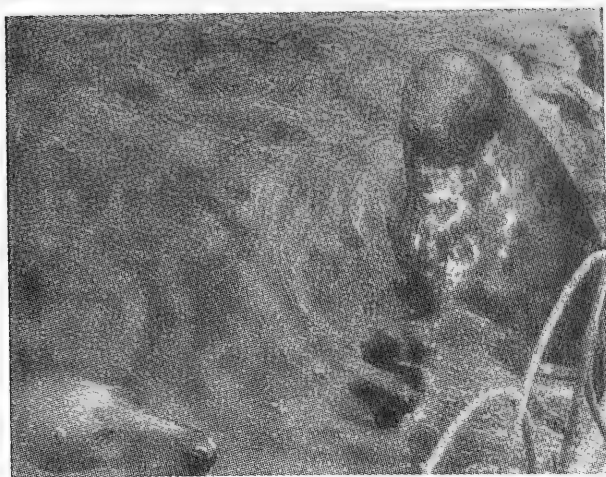
The Baltic zone of distribution is largely isolated from the Atlantic Ocean zone. In the remote past, gray seals resided undoubtedly even in the Denmark Strait and a contact between the populations of the Baltic and North seas did exist though not wholly constant. A real interruption of distribution evidently prevailed for some centuries (for more details, see "Geographic Distribution").

Two subspecies of gray seal can be recognized in our waters at present.

1. **Baltic gray seal or "tevyak,"** *H. g. macrorhynchus* Hornschuh et Schilling (syns. *pachyrhynchus*, *baltica*) (Fig. 190).

The body and skull dimensions are comparatively smaller than those of the nominal form. Sexual dimorphism in dimensions is not very significant. The color is generally very light with fairly bright, though often diffuse, contrasting spots on the chest and neck with relatively less variation. There are practically no animals in the population with intensely dark, almost black coloration. Sex-related color differences are relatively insignificant.

It occupies Gulf of Finland and the waters of Estonia, Latvia, Lithuania, and Kaliningrad district.



353 Fig. 190. Baltic gray seal. Leningrad Zoological Garden (photograph by K.K. Chapskii).

Outside the USSR, the Baltic gray seal is found in the rest of the Baltic Sea regions. The form differs not only in morphological, but also in its biological relation with ice floes on which it breeds (pagophilic form).
 354 2. **Atlantic gray seal or "tevyak,"** *H. g. grypus* Erxleben, 1777 (syns. *griseus*, *gryphus*, *halichoerus*, *gris*, *thienemanni*, *atlantica*) (Fig. 191).

The body and skull dimensions on average are slightly larger than in the preceding form and sex-related size differences are more significant.

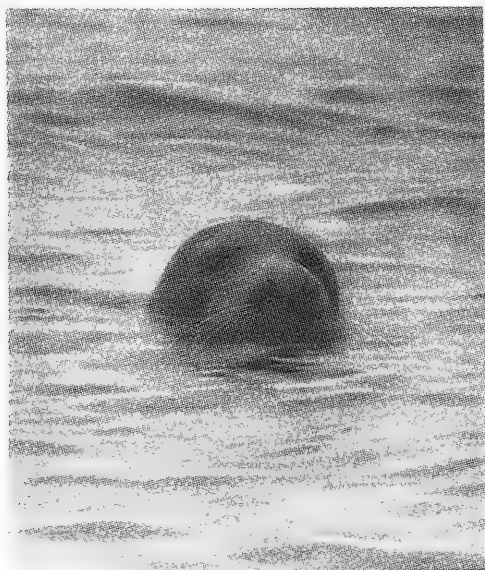
The color on average is darker with somewhat less sharp and contrasting but extremely variable spottiness. Animals are encountered with very dark, almost black coloration. Sex-related color differences are more intense than in the preceding form.

It occupies the Murman coast.

Outside the USSR, this subspecies is found in the rest of the area of distribution of the species, at least in the European waters in addition to the Baltic Sea.

Seals of this form exhibit no affinity for ice floes during the period of breeding (littoral form).

Assigning the nominal name of the subspecies to Murman and generally to the European seals of the oceanic waters is presently still tentative since the waters of southern Greenland represent the terra typica of this form. It may be assumed that the animals existing there are identical with the American form. However, a comparative systematic analysis of the European and American gray seals has not been attempted to date. Yet, while taking into consideration the quite complete (though not absolute)



354 Fig. 191. Murman gray seal in water. Great Ainov Island, Murman coast, May, 1964 (photograph by V.D. Kokhanov).

isolation of these two large populations, it must be considered that they are not identical at the subspecies level. If this is so demonstrated, the name *grypus* should be given to the American gray seals while their European counterpart should be designated by the closest recent synonym.

Nevertheless, the systematic homogeneity of the American form may give rise to some doubts since its composition includes pagophilic as well as aegialoid [littoral] populations. It is possible that some differences do exist between the various populations of seals in European waters.¹²³

Outside our waters, these animals are not classified into particular subspecies.

Biology

Population. Even an approximate census of the population has not been possible in our Baltic Sea waters. It was difficult to establish even the relative sizes of the local populations. Evidently, these seals are least numerous in the easternmost portion of the Gulf of Finland in the region of Vyborg (Freund, 1933). In Nevsk Bay only rarely are stray young

¹²³ According to the latest data (K.K. Chapskii), fairly stable craniological differences do exist between the Atlantic and Baltic subspecies.

seals encountered and that, too, only in the summer-autumn season; the population increases westward. This seal is regarded as common in Estonian waters.

355 In the Gulf of Riga it is relatively more numerous around autumn, especially during the formation of ice floes, in search of which the seals traverse Irben Strait (Aul, Ling, and Paaver, 1957). South of the inlet into the gulf their number decreases sharply down to rare single animals for many kilometers of the coastal zone. The nature of the coastal zone, especially the ruggedness of the coastline, and also the extent of human habitation and hunting activity—all these greatly influence the population of this seal.

The numerical strength of the local seal population changes sharply in different seasons of the year; thus a greater concentration of the seals occurs in the period of breeding and a sparse population in the feeding season. Factors such as the formation of ice floes, their distribution and suitability for whelping, as also the availability of food play a decisive role.

While conducting a census of the world reserves of the gray seal, the strength of the Baltic Sea population was also evaluated. This evaluation was mainly based on information regarding the number of animals killed. The statistics were incomplete because of the nonavailability of data for our waters. In the first evaluation of the world reserves of gray seals (Lockley, 1954), a figure of 5,000 was cited for the Baltic population, exclusively for the Gulf of Bothnia. The view was later expressed that the total reserves in the Baltic Sea should be in the tens of thousands (Davies, 1957). Practically, however, in subsequent evaluations the total Baltic population was roughly put at 10,000 (Haglund, 1961) or 5,000-10,000 (Hook, 1964*; Curry-Lindahl, 1965). A more realistic figure lies between 7,000-10,000.

With this background, it is as yet difficult to reckon the population in the waters of the USSR. According to preliminary data (1972), the mother population of our gray seal in the main region of its winter-spring concentration, i.e., in Irben Strait with adjoining sections of the Gulf of Riga, was roughly put at 350-400. In our zone of the Gulf of Finland, however, the strength is a mere 50 (V.A. Zheglov).

The total strength of our Murman population was put at 300 in foreign compilations (Smith, 1966*). A direct count of the newborn on all the islands of the archipelago of Semi Islands and on the Ainov Islands in the early 1960s identified a total of 200 seals. By applying the method of extrapolation to other regions in which breeding is wholly likely, the total population of annually reproducing females of gray seals has been put at 500-800 (Kandalaksh Sanctuary; Karpovich, Kokhanov

and Tatarinkova, 1967). The main population (without pups) of Murman seals constitutes roughly 1,500.

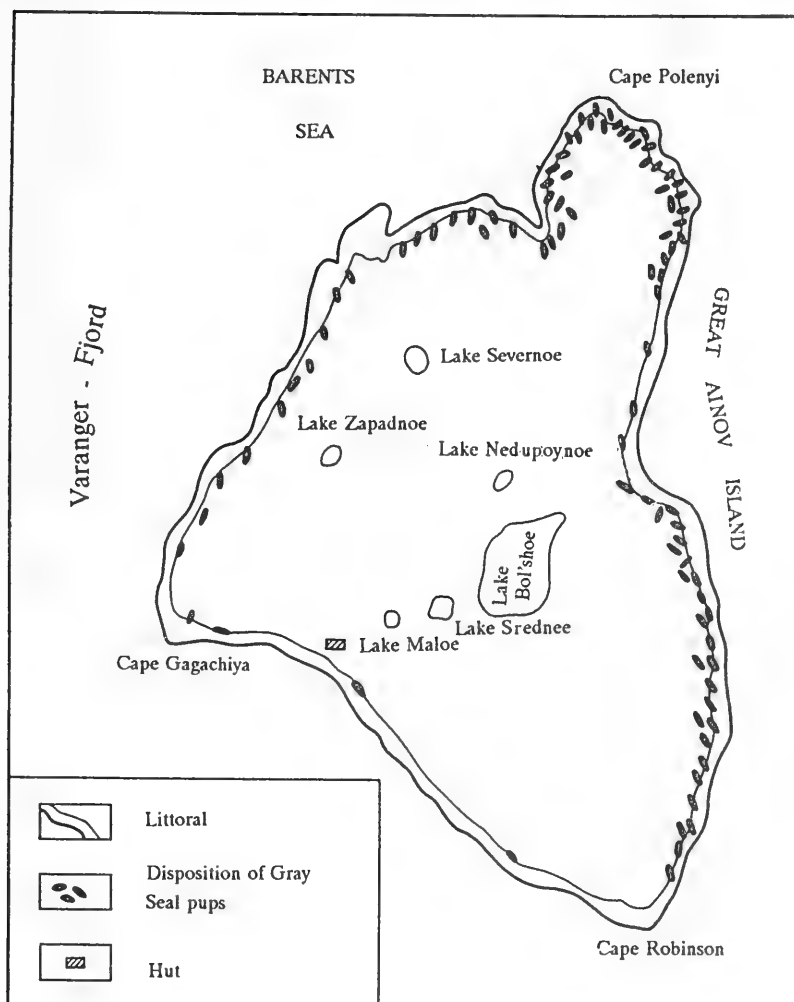
The population of the gray seal in other sections of its range is as follows: 34,000 in the waters of Great Britain of which 5,000 to 8,500 seals are concentrated on the Orkney Islands, Northern Rona, Outer Hebrides, and Farne Island; 2,000 in Irish waters; and 2,000 on the Norwegian coasts. The population of Iceland has been put at the same number as on the Norwegian coasts and on the Faeroe Islands at 3,000. On the whole, for the eastern Atlantic part of the area of distribution there are 42,500 seals (not counting the Baltic Sea and Murman population). In the western Atlantic (American) part of the distribution, the total population runs roughly into 5,000, of which 3,000 are in the Gulf of St. Lawrence and 2,000 east of Nova Scotia (Smith, 1966*). The total world reserves of gray seals thus come to 55,000-60,000.

Habitat. The habitat is closely associated with ecology, which for this species is of a twofold nature, as in the case of seals of the subgenus *Phoca* s. str. (common seal and larga). In our, as well as in international
 356 waters, there are two ecological forms of the gray seal. One of these is biologically associated with the ice floes on which they breed and molt. These are typical pagophilic (ice-loving) animals. This form includes seals of the Baltic Sea and the Gulf of St. Lawrence. The seals in the rest of the European region, including our Murman population as also some populations of the Nova Scotia Islands, reproduce on the coasts. In this season they form fairly cohesive rookeries at definite places on the coast year after year and can be regarded as wholly pagophobic. It is usually assumed, although not always justified, that the pagophobic populations of gray seals are more stationary and reside longer on the same sections of the coastal zone, usually not straying far into the open sea. For rookeries, they select uninhabited, predominantly small islets, inaccessible to man, and made up of smoothly rolled rocky or more rarely pebbly coasts with a flat and fairly level surface. They are disposed right on the coast, slightly above the littoral zone as well as away from it in the more elevated sections, including those overgrown with grasses.

Usually, the flat rocky coasts of islands slightly above the line of high tide serve as the site of whelping on Murman but at times the semisubmerged littoral sections are also used (Fig. 192); a distinct preference is
 357 shown for smoothly-rolled boulders. Sometimes the ascent of the coast is quite steep (up to 30° or more) but matters not if it is smooth. It is not important how much of the slope is covered with a thick layer of snow. Beaches with boulders or pebbles are rarely selected for whelping (Uspenskii, 1941; Karpovich, Kokhanov and Tatarinkova, 1967). On the

Great Ainov Island (in the region of Varanger Fjord), the sites of whelping fall predominantly in the littoral zone toward the open sea but are almost wholly absent on the southwestern side turned to the mainland coast. Often, they are disposed there in sections with peat clumps among tall grasses (lyme grass) (V.D. Kokhanov).

Our Baltic pagophilic populations during the breeding season are disposed close to the outer rim of drifting ice floes, abounding in fissures,



356 Fig. 192. Figure showing the disposition of newborn gray seal pups on Great Ainov Island, Murman coast, November - December, 1963 (after V.D. Kokhanov).

open water pools, and partings, which are essential for keeping contact with the water. Only in very rare cases, when the winter is extremely mild, do some animals use the coastal rocks for whelping (Curry-Lindahl, 1965). Under the influence of ice floe movements, the fissures developing among them, and the expansions and contractions of the open water pools, considerable changes occur in the original distribution of the new-borns over the course of time: some pups and their suckling mothers drift with the ice floes to the very edge or sometimes deep into the ice massif, thereby being islanded in the dense ice "conglomerate".

The Baltic seals are usually regarded as more pelagic (Curry-Lindahl, 1965) than the British animals whose coastal rookeries in summer are very specifically fixed.

Food. In our waters this aspect has been thoroughly studied only recently. There are practically no definitive data on the food of the Murman gray seal. Judging from observations, however, lumpfish and cod assume a prominent position in its food (V.D. Kokhanov). Only general information is available on the food of the Baltic gray seal. On the coasts of Estonia, it feeds on Baltic herring, cod, viviparous blenny, eel, salmon, and bream (Aul, Ling, and Paaver, 1957). The animals held in the Leningrad Zoological Garden (caught in the Gulf of Riga) consume diverse fresh fishes from the Gulf of Finland and Lake Ladoga including such freshwater fishes as roach, ide, dace, rudd, bream, etc. In nature, at February end to early March, 1972, only the remnants of benthic fish, i.e., viviparous blenny and flounder, were found in the stomach of whelped females of the Baltic population (V.A. Zheglov).

The gray seal of the west European and Canadian populations is usually regarded as a consumer of predominantly a wide variety of fishes. The instance of catching a seal on a baited hook dropped to a depth of 145 m and also the repeatedly reported facts of the emergence of these seals with deep-water fish between their teeth (Collett, 1881), point to the possibility of these seals "fishing" at considerable depths. In the European seas the gray seals consume, in addition to the above-listed fishes, halibut, other flounders, herring, ling, whiting, and other cods and pike. Apart from fish, they catch cephalopod mollusks (squids—*Loligo forbesi* and *Eledone cinerosa* were noticed in the Irish Sea) and at times consume even deep-sea crustaceans (Collett, 1911–1912; Freund, 1933; Duncan, 1956; Lockie, 1962). In the stomach of some tens of gray seals caught in the Gulf of St. Lawrence, the following were identified: among fish—mackerel (?), cod, herring, salmon, hake, small winter flounders, unidentified species of flounders, skate, and shark; among invertebrates—squids, crabs, and shrimps (Fisher and Mackenzie, 1955; Mansfield, 1966).

The diet of the gray seals varies considerably depending on age, season, and local conditions. These factors are also responsible for the magnitude of losses suffered by the fishing industry (see p. 495). According to some sources, the gray seal is such a voracious eater that it can consume its own weight in fish in a single day in captivity (Legendre, 1947). The daily ration of caged gray seals abroad is 6.8 kg (Steven, 1934, 1936). They receive a slightly larger ration in the zoological gardens of Leningrad and Kaliningrad where the seals enjoy good health.

The stomach of one animal shot contained 27 completely whole eels that had evidently been swallowed in a very short period of time (Curry-Lindahl, 1965). In another animal 54 common perch and one pike, in addition to several herrings, were found in the stomach; it was said that an adult seal can consume 60 to 80 herrings daily (Friedel, 1882). However, it should be noted that, in nature, it feeds at intervals during the periods of reproduction and molt. Evidently lactating females feed sporadically, with intervals of starvation occurring during the summer-autumn season.

When the fish is large (not in the case of an eel), the gray seal tears it apart with the claws of its fore flippers and consumes it in bits. Smaller fish, such as the herring as well as the eel are swallowed whole (Nehring, 1887). These habits have been recorded during the food intake of seals at the Leningrad and Kaliningrad Zoological Gardens.

Home range. Historically, each local population has maintained a fairly stable home range. This is primarily and especially true of pagophobic populations. Observations of the British-Irish populations have established that the bulk of the mother population whelps year after year on the same coastal section. Nevertheless, the animals are not confined to the same site year round. Even the most settled among them abandon the rookery at the end of reproduction, lactation, and molt, wandering from place to place along the coastal belt. Therefore, establishing the dimensions of water bodies covered by a given group or a single animal is a difficult task.

The Murman seals lead a more stationary life. They are distributed in different regions of a comparatively narrow coastal strip as fairly distinct isolated local groups living in herds. Such conditions make it wholly possible to determine the home range areas of the seals in future. Stray animals are, however, encountered close to Mezensk Bay.

The Baltic gray seals, on the other hand, reveal a varying affinity for given sections of their habitat. In the winter-spring period, when they are confined to ice floes, mainly close to the edges, the area occupied by them often varies in accordance with ice floe drift. Thus the area of occupancy is sometimes more, sometimes less. Under these conditions,

the density of disposition of the seals is highly variable not only from year to year, but also in the relatively short icy season.

During the periods of reproduction or molt the seals on ice floes generally do not gather into groups; instead they scatter, sometimes at considerable distances from each other, although not as far apart as in the case of the larga at this time in the Bering Sea (see p. 353-354). But sometimes the animals do gather in a small section of the ice floe or even in groups forming small rookeries. At this time the concentration of gray seals is maximum. According to recent observations, gestating females are disposed quite often in small groups of two-five or large groups of 20-40 animals; sometimes they group in even larger numbers or remain singly (V.A. Zheglov).

At the end of the reproduction and lactation period, the adult seals that have mated do not evidently go into the water nor do they abandon
 359 the region of whelping; the seals begin to molt. The well-fed pups also remain on the ice floe for some time more until the embryonic hair coat has been completely shed. After the disappearance of ice floes in the summer-autumn season, the seals scatter in a wide expanse and keep moving in search of food for much of the time.

Hideouts and shelters. The gray seal organizes no special protection for the pups born even on ice floes or on snowbound land. The newborns lie in the open and only sometimes, as for example on the islands along the Murman coast, especially on Great Ainov, enjoy the protection of a projecting stone or a peat clump (V.D. Kokhanov). Information on the disposition of pups on ice floes in the Baltic Sea has only begun to be collected (V.A. Zheglov).

For a long time there was no unanimity of opinion regarding the ability of the pagophilic gray seals to make air holes in ice floes for communicating with the water. According to some (Holm, 1921; Aul, Ling, and Paaver, 1957), the seals do make air holes and keep them open. One such hole is sometimes used by many animals. Curry-Lindahl's (1965) reports do not confirm this view. There is no need for the gray seal to make air holes as the whelping site in the fringe zone of drifting ice floes already has innumerable open water pools. Evidently, they set out to make air holes only when needed, i.e., when the open water pools or an enlarged fissure is covered by a recently formed ice crust.

Daily activity and behavior. The daily cycle of activity and the behavior of the Baltic gray seals have not yet been studied thoroughly.

In general, the gray seal is a fairly gregarious animal but its herding instinct is not equally well developed among the ecologically different populations; among the pagophiles, especially the Baltic seals, this tendency is weaker than among the land seals. The herding reflex evidently

peaks by the time of reproduction. However, some British rookeries exist long before or after the breeding period or there are those in which the animals do not reproduce at all. The same is noticed among Murman gray seals, which quite often are bound in herds on their favorite sites on islands after the breeding season.

The regime of the coastal rookeries also varies. Some exist for a long time and even almost uninterruptedly round the year, as for example on the small islets of St. Kilda to the extreme west of the Hebrides (Waters, 1965). Others, however, function for a much shorter period or are characterized by almost uninterrupted traffic for the reason that all the females do not arrive at the same time and remain on land for 2-3 weeks after whelping, their pups for an average of 4-5 weeks (Fitter, 1961), and later leave the rookery altogether. The coastal collections of animals also vary widely in size: in the British Isles the sizes vary from small groups of a few tens to huge herds of 2,000 or even up to 5,000 seals. During the periods of reproduction and feeding, the animals of different ecological groups are active during the day as well as at night except for hours of sleep, for which there is probably no fixed time schedule. These seals can sleep in water as well. Activity and ability of orientation and finding food at night are characteristic of the Murman gray seals who have lived long under conditions of the polar night, coinciding with their period of reproduction. Activity of the British gray seals right up to their successfully catching salmon in the dark has been confirmed by observations on the east coast of England in the estuary of Tweed River (Rae and Shearer, 1965).

During their residence on the coastal rookeries for reproduction in our Murman region as well as in British waters, the seals do not generally feed. During lactation the whelped females of the Murman population remain silent in the water not far from the pups lying on the coast, always ready to respond to the pup's call. Less often, they spend the intervals between sucklings on land near the pups. The nurseries there, as at other places, break up as the well-fed pups begin to enter the water. A part of the population abandons the reproductive section while others remain for a longer period, until spring, and a very small number even up to summer; at this time, the seals remain in groups in the water. In spring, coastal rookeries are often formed there again. A characteristic features of these rookeries is that the seals are disposed in clusters, quite close to each other (Karpovich, Kokhanov, and Tatarinkova, 1967).

Seasonal migrations and transgressions. The seasonal migrations of the gray seals do not exhibit similarity in magnitude or regularity with those of the harp seal, hooded seal, or fur seal. Some remote similarity of these migrations is seen only with the Baltic gray seal.

The magnitude of migrations and the duration of residence in the sea and the density of animals of different age groups and in different sections of distribution (with varying extent of food availability) differ among the pagophilics and land seals. It is known that the young of the British population remain continuously at sea for the first two years, often quite far from the site of their birth (Davies, 1956*).

In the winter-spring period, like the harp seal, but on an extremely small scale, the bulk of the gray seals concentrate in relatively limited sections of distribution where the ice conditions are most favorable for reproduction and later even for molt; at the end of this season, however, they return to the extensive feeding expanses. Thus, on our Baltic coasts, in the winter-spring season, the gray seal is usually confined mainly to Irben Strait and the western regions of the Gulf of Riga. In the ice-free period, however, these seals are more widely scattered.

The main impetus for the spring-winter migrations is the need for finding suitable ice floes that ensure dependable conditions for raising the offspring. The seals seek out stable, white, coarsely broken ice floes that are not intensely hummocky and with a fair amount of open water pools. The selection of Irben Strait for this purpose is wholly justified since suitable conditions required for whelping and lactation are generally available there. The seals find similar conditions also in the central eastern section of the southern strip of the Gulf of Finland. Regions of their breeding are also known outside our territorial waters. The seals begin to move to the breeding zones by late autumn, the younger animals migrating somewhat earlier (Holm, 1921). In the wintering site, they are seen in clusters by December, sometimes even in November.

By March end to early April, at the end of the breeding season, the adult animals leave the suckled pups on the ice to complete molt and begin to return to their summer habitat. Initially, this process is passive with the drift of ice floes but later becomes more active.

The Murman gray seal, having lost its biological link with ice floes, has become a more settled animal. For three-fourths of the year, from August end, the whole of autumn, winter, and spring months, its population, with some minor changes, is confined to the Semi and Ainov islands. In the former region the seals may be seen even in spring (before June) in herds of 20-70 animals or more on Litskie, Veshnyak, and Kuvshin islands and also in some sections of the mainland coast where they form fairly dense rookeries in spring. Such groups of gray seals are seen at this time on the Ainov Islands also. But most of the animals depart in June and only rare strays continue to remain until the end of August. The summer habitat of the bulk of the seals is not known for certain. They

361 begin to return to the sites on the Semi and Ainov islands by autumn, from the end of August (Karpovich, Kokhanov, and Tatarinkova, 1967).

In the context of seasonal migrations of Murman gray seals, the corresponding process among their kin, especially the British populations, is of interest. There are no essential differences in this respect between many British and our Murman populations. The seals remain throughout the year in the waters of western Wales, migrations here being only of local interest (Lockley, 1954). The British populations are sometimes classified as nonmigratory (Davies, 1956*). However, massive tagging of pups, commencing in 1954, has shown their great capacity to migrate and for distant transgressions. Although 85% of a batch of pups marked on Farne Islands did not leave the area of their birth, some were caught on the coasts of Holland, the Federal Republic of Germany, and Denmark, while some reached Norway and the Faeroe Islands (Hickling and Ennion, 1959*). New data (tagging at the commencement of the 1960s on the Orkney Islands) confirmed the extensive scattering of juveniles, including even Norway where some twenty tagged animals were recovered from 1960 through 1962 (Hickling, Rasmussen, and Smith, 1962). While these do not represent systematic distant migrations, they confirm the great mobility of the juveniles and their ability to negotiate long distances. This has been convincingly demonstrated by the fairly extensive actual exchange even between isolated populations, which appear extremely remote at first glance (see p. 488).

Reproduction. The period of mating among this species extends on the whole for almost three-fourths of the year, from July end to March end or early April while some animals mate even somewhat later. Such a wide mating season is explained partly by the fact that the animals belonging to the ecologically different groups have their own periods of mating, partly due to extensive population variations at these periods among the seals in the British part of the distribution.

The Baltic seals reproducing on ice floes mate in early spring, mostly in March (predominantly at the end of this month) or in April; it is possible that mating occurs at a much earlier or even at a later period, however, in February (Lilljeborg, 1874; Freund, 1933), May (Nehring, 1886), and even in June (Neif, 1757*). It has further been pointed out that in the more northern Baltic regions, especially in the Gulf of Bothnia, the seals mate later (in June) than in the Gulf of Finland. According to the latest data (V.A. Zhegllov), the period of mating in Irben Strait extends from around March 10 to mid-April.

In the Baltic Sea the seals concentrate for reproduction in a fairly restricted strip of coarsely broken fringes of ice floes, usually tending in March to south of the Aland Islands, mainly in a latitudinal direction,

forming a deep loop in the Gulf of Finland. In the southern part of the Gulf of Bothnia extensive air holes become available by this time but whether the gray seals remain in the gulf or reproduce along its periphery is not known. In general, however, the disposition of the massive drifting ice floes suitable for whelping is highly variable not only in a given season, but also in different years. In such situations there is little justification for assuming fixed dispositions of productive males and the mother population with pups or the existence of sharply isolated populations. The affirmation that there are no definite places in the Baltic Sea where these seals can be found for certain in the season of reproduction or molt is not mere speculation (Smith, 1966*). Nevertheless, judging from the data of recent years (V.A. Zheglov), the stable regions of reproduction in our waters are Irben Strait as well as the predominantly western part of the Gulf of Riga. A very small portion of the population breeds in the central and eastern regions of the southern part of the Gulf of Finland.

362 Not much is known about the nature of the mating period. Nevertheless, in spite of statements to the contrary in the literature (Curry-Lindahl, 1965), harems are not a characteristic of the Baltic seal. The seals mate two weeks after whelping. Copulation occurs in water as well as on ice floes but more often evidently in water. Among the British gray seals, there is a definite relation between the nature of coitus and the extent of manifestation of the harem regime in the rookery. On land, these seals mate at places where the males hold firmly to their territorial sections, as for example in the largest rookeries on the northern Rona and Farne Islands. But even under these conditions, when fairly deep erosion "tanks" or "channels" are available, the animals eagerly take advantage of them for coitus. When, however, the males are confined preferentially to the sea in front of the whelping site, mating proceeds in water (Hewer, 1960). Under the prevailing harem regime of the rookery, the males holding onto a definite territory fertilize many females. Evidently, in water too, the more powerful males stand in an advantageous position by chasing away the much younger and weaker animals.

This aspect of the life of Murman gray seals has not been clearly understood. In the Norwegian waters in the remote past, when the seal population was much larger, there were 2 to 4 or 5 females to every bull (Collett, 1881). Murman gray seals mate late in the autumn and early winter, 2 to 3 weeks after whelping or slightly later. This period essentially falls at the end of November to the end of December. Any overture to mating before this period (long before completion of lactation of the female) or male proximity to her pup is decisively resisted by the suckling female, even to the extent of biting the neck of the intruder. Mating

is completed mainly on land. In any case, mating in water could not be observed. Coitus is preceded by conjugal play in water or on the coast when the animals gently bite each other. Signs of distinct harem formation were not seen among the Murman population nor were there more females than males among the adult animals. It is nevertheless possible that both monogamy and polygamy prevail on Murman. Polygamy was suggested by the disposition of pups in groups of 2-4 together (Karpovich, Kokhanov, and Tatarinkova, 1967).

Conforming to the extended period for mating, the whelping season too reveals wide variations geographically as well as among the various seal groups in the same region. Thus, in the Great Britain-Ireland region, some main groups in the population have a much extended whelping period while others have a short whelping period. In Wales, the Irish Sea, and on the western coast of Ireland, whelping extends from July through October; among Scottish-Hebrides populations, pups are encountered in September-October and on the Farne Islands (northeastern coast of England) from the second half of October to the middle of December (Coulson and Hickling, 1964). However, the bulk of the females whelp within a very short period of about a month. The view that the eastern Atlantic seals whelp increasingly later toward the south (Mohr, 1952) has not been fully substantiated.

The Murman seals are distinguished by a somewhat greater stability in this respect: the period of reproduction among them extends for not more than 1.5 months in the late autumn. Even according to older information (Prigorovskii and Breitfus, 1912, 1915), newborn pups of gray seals were caught on Murman throughout December but, according to much later information, they were seen on the Semi Islands in early November (S.M. Uspenskii, 1941), from the end of November to the end of December (Sdobnikov, 1933*); they were caught on November 16 and 17, December 6 (Belopol'skii, 1941) or in November and December (Belopol'skii, 1951). The above whelping periods in eastern as well as western Murman have been confirmed by the latest observations; they
363 are identical and the total duration of whelping extends for 30 to 40 days. The earliest pups are born in the first ten days of November and the last ones toward mid-December. In 1963, on Great Ainov Island, two peaks were noticed in the birth of pups, one from November 10 to 15 and the second, a sharper peak, at November end to early December (Karpovich, Kokhanov and Tatarinkova, 1967).

Though neither the whelping nor mating season of the Baltic seal as reported in the literature is very accurate, there are no particular disparities regarding these aspects. In most cases the pups appear by February to March, the main whelping season falling in March (Lilljeborg, 1874;

Nehring, 1886; Aul, Ling, and Paaver, 1957) or February end to early March (Holm, 1921) or between February end and mid-April (Smith, 1966*). Recent observations have shown that the total whelping period among the Baltic gray seals extends for one month from around February 20; most of the pups are born from February end to March 4-5 (V.A. Zheglov).

The gestation period has been put variously at 8.5 to 12 months because of the lack of accurately established mating and whelping periods. In the middle of this century, it was assumed as 11 months, as in the case of other seals (Mohr, 1952). Obviously, however, the entire period from mating to parturition stretches two weeks longer, to 11.5 months. But considering that a prolonged delay of zygote implantation is characteristic of gray seals (Lockley, 1954; Backhouse and Hewer, 1956), the actual embryogeny extends for roughly nine months or so.

The birth process is extremely brief, being accomplished in a few seconds; the placenta is discarded in an hour and many animals eat it (Matthews, 1952). Twins are very rare among gray seals (Collett, 1881; Curry-Lindahl, 1965) although according to some authors (Aul, Ling, and Paaver, 1957), Baltic seals do produce twins.

Births in the normal course are an annual feature. The overall barrenness has not been established accurately for any of the populations of these seals though the quantum of females not participating in reproduction, on analogy with fur seals, was put at 20% among the British population (Hewer, 1964).

The British female gray seals become capable of reproducing partly (50%) at five years of age and wholly (100%) at six years. By this time, depending on the state of ovogenesis and ovulation, the length of the ovaries increases on average by 32-35 mm and the weight goes up to 5-8 g. Thus the female births her first pup at six years of age. The males become mature at seven years of age but stake their claim at the site of reproduction only on attaining 10 years; they cease mating at 20 years of age. Among mature males, in the mating season, the weight of the testes together with the spermatic cord varies from 100 to 290 g, on average 166 g. The weight decreases by the end of the mating season roughly to 100 g; the length of the os penis is not less than 10 cm.

The females remain productive for a very long time; although rare, gestating females older than 30 years (31-32 years) have been recorded. The oldest female encountered in a breeding site was 33-34 years (Hewer, 1964).

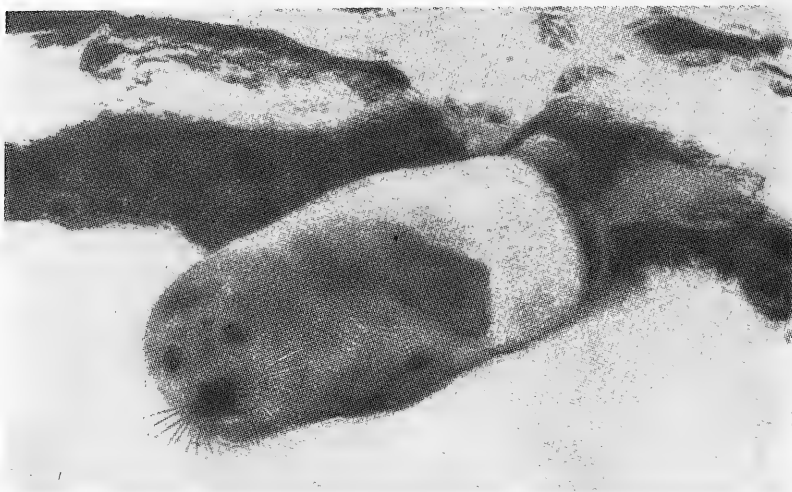
Similar data are still not available for Murman gray seals. The oldest suckling Baltic seal seen in our waters was aged 21 years (V.A. Zheglov).

*Growth and development*¹²⁴. There is very little concrete information on the size of newborn pups of Baltic seals in the earlier works. The following figures are cited: 95 cm (Lilljeborg, 1874) and 60 cm (Priemel, 1909). The first figure is wholly reliable (evidently, the pup was measured along the dorsal surface) while the latter figure is clearly an undermeasurement. According to the current data (V. A. Zheglov), the body length in a straight line (i.e., *Lcv*) varies from 75 to 85 cm and along the dorsal surface (*Lc*) from 82 to 92 cm; weight ranges from 6.1 to 9.5 kg, on average 8.15 kg. The length of the suckling pup averages 100-110 cm or 110-120 cm (*Lc*) and its weight 40-50 kg (the lower limit pertains to females and the upper limit to males). The body length of a newborn Murman female gray seal in a straight line (*Lcv*) is 107 cm, axillary girth 64 cm, thickness of the skin with the subcutaneous fat layer (*St*) 0.5 cm; total weight 15.2 kg (Uspenskii, 1941). A slightly older male pup, roughly three days old, was 110 cm long (*Lcv*) with an axillary girth of 66 cm, thickness of skin (*St*) 0.9 cm, and weight 20.5 kg (Fig. 193). Pups born with a body length (evidently, *Lcv*) of 80-107 cm add 15-25 cm in the period of suckling, the most intense growth occurring in the first two weeks. After 5-7 days the canines have cut through and the rest of the permanent teeth are cut immediately afterward (Karpovich, Kokhanov, and Tatarinkova, 1967).

The newborn British seals weigh 11.5-17.5 kg but most 14-16 kg, with a body length of 91-108 cm; the body weight increases during the period of lactation to 40-50 kg (Matthews, 1952; Coulson and Hickling; 1964). The duration of lactation has been recorded by various authors as two weeks (Darling, 1948) and four weeks (Lilljeborg, 1874). Evidently suckling most often ceases in the middle of the third week (captive pups were weaned on the 18th day, and on Farne Islands, England on the 16th day) (Coulson and Hickling, 1964). During the first three days of lactation the daily weight increment averages 1.5 to 1.8 kg. This rapid increment in weight is ensured by the high fat (52% or more) and protein (11%) contents of the mother's milk (Amoroso and Matthews, 1951).

The frequency of suckling (Fig. 194) changes with time. The newborn receives its first nourishment 30 min after birth and later at 2-hr intervals; in the latter days this interval increases and the number of feeds decreases to a few times a day (Smith, 1962). Among the Baltic seals, the

¹²⁴ The data available in the literature on the size of the newborn, its growth during the period of lactation, and in the subsequent period of its independent living, at least in the first year, as well as the sizes of adults are difficult to utilize since it is usually not known how the animals were measured: along the dorsal curvature or in a straight line to the tip of the tail, or to the end of the extended hind flippers.



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Fig. 193. Newborn pup of Murman gray seal in the first few days after birth. Great Ainov Island, Murman coast, December, 1963 (photograph by V.D. Kokhanov).

pups suckle initially at 3-4 hour intervals, receiving 400-650 g or more of milk in each feed. The daily weight increment varies from 1.2 to 2.5 kg but most pups double their weight in 8-10 days and reach 33-40 kg or more by the end of the lactation period (V.A. Zheglov). The suckling duration increases as the pup grows and the milk intake likewise increases. According to observations on Great Ainov Island (western Murman), in the second half of the lactation period suckling extends for almost 15 min. The pups suckle the two teats alternately, taking 3-4 mouthfuls at a time from each (Karpovich, Kokhanov, and Tatarinkova, 1967).

The behavior of pups of the Murman population in the period of suckling has been described as follows: "The newborn pup moves little and permits fondling with the hand with no resistance. Just a few days later, it becomes active and attempts to shy away from man or protect itself, sometimes by trying to attack". The pups usually remain within the coastal belt, up to 100 m from the line of high tide. Sometimes, however, they do stray up to 300-400 m beyond the coast. The pups spend much of the first two weeks sleeping, mostly on the right side or on the back. With the commencement of intense molting, they become more active, mainly on the rocks, often descending into the pools in the sublittoral and littoral zones. Some pups still not completely molted go into the sea (Karpovich, Kokhanov, and Tatarinkova, 1967). Completely molted pups, however, continue to remain on land for a few more days,

often moving away for long distances from the place of birth, or migrate from one island to another in the vicinity (Karpovich, Kokhanov, and Tatarinkova, 1967).

The pup retains its white embryonic coat for the same short duration on the ice in the Baltic Sea as well as on the Murman islands, Norway or Great Britain. This coat loses strength in seven to ten days (Neif, 1957*; Collett, 1881; and others); among Baltic Sea newborn males and females, this happens in 5-6 and 8-10 days respectively. In 17-20 days hair begins to appear again on the trunk (V.A. Zheglov). Among Murman gray seal juveniles too molting is over by the end of the first week. The first molt follows a fairly common pattern for all the animals of the family. Weakening and shedding of the embryonic hair coat usually occurs first on the head, the hind and fore flippers, and the tail (Fig. 195). On the 5th-8th day the embryonic coat thins out on the snout and on the flippers; dark spots show through the embryonic coat here and there on the back. On the 9th-12th day dark spots are seen all over the body, which fuse into a continuous gray field, signifying the commencement of intense molting (Fig. 196). By the 13th-16th day the head, back, and sections around the flippers have completely molted and the embryonic coat elsewhere on the body scales off intensely. On the 17th-22nd day hair remnants are seen only on the flanks and on the abdomen but these too are weak; on



Fig. 194. Posture of gray seal during suckling. Great Ainov Island, Murman coast, December, 1963 (photograph by V.D. Kokhanov).

the 23rd -24th day the remnants are rare; on the 25th - 27th day there is nothing left of the embryonic coat and the pups appear in the new coat with smooth short hair (Karpovich, Kokhanov, and Tatarinkova, 1967) (Fig. 197). Thus the entire molting process in Murman takes roughly three weeks. Little is known in general about the further growth of the juvenile. There is altogether no information on its life and growth tempo in our territorial waters. On taking to independent living in water, the pups are usually scattered widely, quite often straying very far from the place of their birth (see p. 481). The subsequent growth of the juvenile has been studied only among the British populations; by the end of the first year, the males begin to outstrip the females in growth (Table 26).

The yearlings are practically no different from the well-fed pups (at the time of first molt of their embryonic coat) and are even lighter in

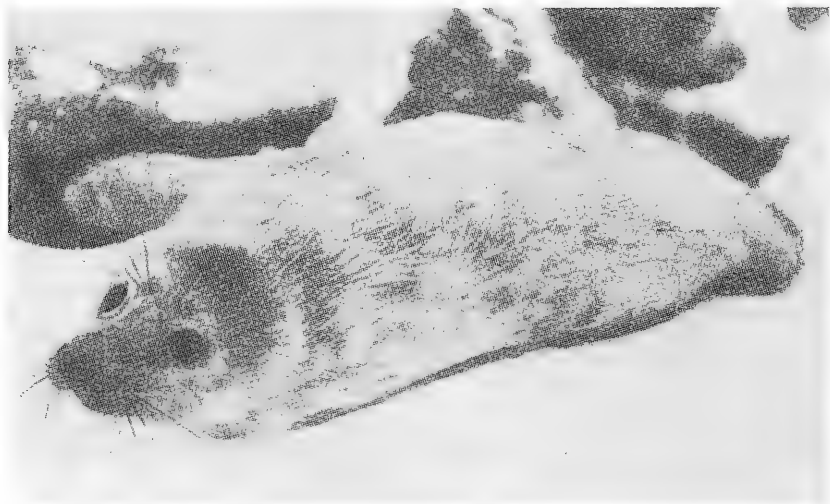
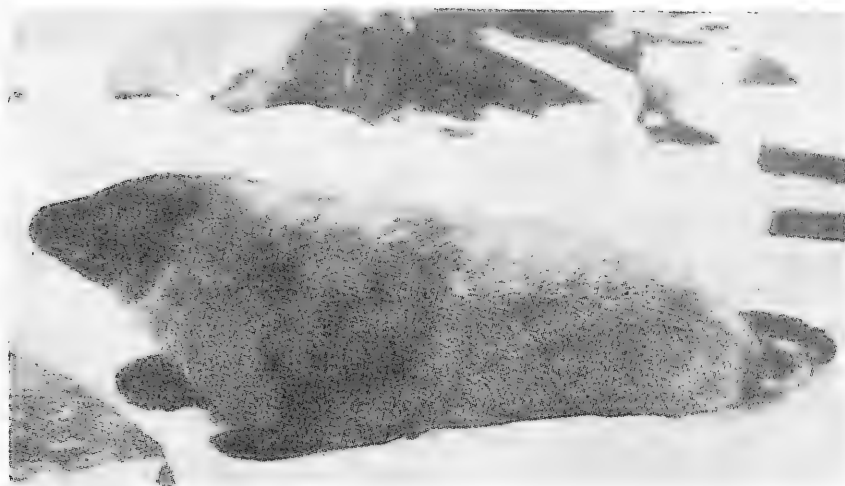


Fig. 195. Some growing gray seal pups; commencement of molt. Great Ainov Island, Murman coast, December, 1963 (photograph by V.D. Kokhanov).

Table 26. Average body weight (after Hewer, 1964)

Age, in years	Average body weight (approximate), kg	
	Female	Male
1	41	42
2	49	59
3	55	74
4	65	90
5	72	105



366 Fig. 196. Molting gray seal pup. Great Ainov Island, Murman coast, December, 1963 (photograph by V.D. Kokhanov).



367 Fig. 197. Molted gray seal pup. Great Ainov Island, Murman coast, December (photograph by V.D. Kokhanov).

weight than the latter. This phenomenon (Coulson, 1959*; Coulson and Hickling, 1964) is explained by the characteristics of the further growth conditions of a pup in the first few months of its independent existence. While still on the ice floes, after lactation ceases, the pup suffers a weight loss which continues for sometime even in the water as the youngster

has to acclimatize and become accustomed to finding its own food. This transitional period is evidently a vital factor in its life (as among other seals) and the pup is often forced to merely survive by expending the reserves accumulated during lactation. The pup can replenish its body losses only after total adaptation to the water and taking to intensive feeding.

The growth of the animals, judging from the growth curve of the British seals (Hewer, 1964), continues with gradual attenuation until roughly 10 years among females and up to 15 years among males, or perhaps somewhat later. The average difference in body length between males and females after total growth cessation is roughly 35 cm. Growth is most intense among females for 6-7 years and among males for 8-9 years. Increase in skull length proceeds roughly in this same range.

The known longevity in nature is 35 years for females and 25 years for males (Hewer, 1964). In zoological gardens some females have survived for 28 and males 41 years (Matheson, 1950; Mohr, 1952).

Information on the molting of adult Baltic seals is very scant. At the end of the period of reproduction, after some nourishment, the Baltic seals return to ice floes and form fairly large molting rookeries on them (Holm, 1921). According to the earlier data (Neif, 1757*), this process commences by March 25; the present information (Curry-Lindahl, 1965) puts the molting of seals in April-May. There is no information at all on the molting of Murman seals.

In British waters the molting period proceeds 1.5 to 2 months after the mating period; females molt much earlier (mainly at January end to early February) than males (mainly in March) (Backhouse, 1960; Smith, 1962).

Enemies, diseases, parasites, mortality, and competitors. These aspects have been little studied in our waters. In the Baltic Sea the eagle may be an enemy of the pups (Aul, Ling, and Paaver, 1957) but these birds are very rare in the pelagic regions of the sea. The pups are probably threatened by large gulls, especially the great black-backed gull (*Larus marinus* L.), which pecks at the placenta and the newborn (V.A. Zheglov). Evidently the pups also suffer from unfavorable ice conditions. Instances of early thawing or hummocking of ice floes can pose mortal consequences for the pups which are yet weak and have not had sufficient time to accumulate the subcutaneous fat reserves requisite for independent survival in water. Ravens pose some danger to the newborn on Murman (Uspenskii, 1941). Recent observations on the breeding sites of the gray seal on Murman have shown that the losses among pups are very few. On Great Ainov Island in 1963, of 93 pups, only two were found dead. Two dead pups were found in the winter of 1960/61 on Veshnyak Island

(Karpovich, Kokhanov, and Tatarinkova, 1967). In the British Isles pups born on the rocks in high-tide areas perish almost wholly; on northern Rona Island, in two weeks of October, pup mortality was 16% (Boyd, Lockie, and Hewan, 1962*). The mortality among newborns in 1957 on the Farne Islands was in the same range (England; Hickling, 1959*).

In calculations of the age-sex structure of the British populations, mortality in the first year was put at 60% of the total population of pups, 30% in the second year, and 12% in the third year; it was 6.7% in each of the subsequent years (Hewan, 1964).

The helminth fauna of gray seals inhabiting the USSR waters has yet to be adequately studied. Gray seals are infected by eight species of helminths, among which not a single cestode appears (Delyamure, 1955); among the trematodes, *Metorchis albidus*, *Opisthorchis tenuicollis*, and *Pseudamphistomum truncatum* infect the gall bladder and bile ducts; among the nematodes, *Anisakis similis* infects the intestine, and *Contracaecum osculatum* and *Terranova decipiens* infect the stomach and the intestine; among the acanthocephalans, *Corynosoma strumosum* and *C. semerme* infect the intestine.

369 The gray seal has no competitor in the Baltic Sea. This is the largest of the marine life normally inhabiting this water body and has its own ecological niche, preferentially confined to the more pelagic regions, and feeding at depth. The common seal in the southern part of the Baltic is much smaller than the gray seal. The distribution of both these species in Murman represents the boundary of the range and both evidently live under different biotopic conditions.

Population dynamics. In the southern parts of the Gulf of Finland the population is insignificant and apparently is continuing to decline. The total population of the gray seal in the Baltic Sea too continues to drop with no remission, especially in the gulfs of Finland and Bothnia. Thus, the average annual catch of both species of seals in Finland compared with the pre-Revolution period, dropped in the second half of the 1920s roughly by 30% and in the early half of the 1930s by as much as 60%. The situation was similar in Swedish waters. The gray seal in the Baltic Sea is largely unprotected from foreign hunters. Encouraged by monetary rewards, they kill it wherever and whenever convenient. Apart from the fact that the seal is intensely hunted in general, significant qualitative changes have occurred in the structure of its population due predominantly to killing of pups in the past as well as now, as they are quite easy to catch (Bergman, 1956). Hence the herd is relatively overloaded with older animals (Curry-Lindahl, 1965) whose natural death cannot be replenished. That the Baltic seal population, which showed some recovery after the war years, continues to fall is supported by the magnitude of

the continuously declining kill in spite of the alluring monetary rewards granted by the Swedish and Finnish governments for every animal killed (Table 27).

Apprehensive of the extermination of the seals, Swedish organizations for environmental conservation have turned to the government with proposals for the abolition of rewards for each killed animal, a ban on hunting during the breeding period, and the establishment of a number of sanctuaries (Curry-Lindahl, 1965).

The small population of Murman gray seals underwent changes in the current century in relation to hunting activity. In the pre-Revolution period and the initial post-Revolution years, the population was evidently at maximum. In the 1930s, as a result of excessive killing of pups, the population fell but was again restored after the years of the Patriotic War. The establishment of Kandalaksh sanctuary played a positive role in sustaining and raising the population. At present, "the population of gray seals in the sanctuary has restored to the levels prevailing in the 1920s" (Karpovich, Kokhanov, and Tatarinkova, 1967).

Field characteristics. The gray seal can be distinguished from other seals by the straight (upper) profile of the head, long snout, and light coloration of the upper portion of the head (Fig. 198). The last feature unmistakably distinguishes from a distance a swimming gray seal from the common seal whose head is invariably dark (Millais, 1904; Collett, 1911-1912). In the Baltic Sea the gray seal can be recognized from a distance by its large size, elongated snout, and coloration, i.e., innumerable dark spots scattered haphazardly on a much lighter gray background; a gray seal protruding above the water can be recognized from the contrasting color of the throat, neck, and chest with a pattern of larger spots seen prominently on a light background. Murman gray seals can also be identified by these features as well as by the dark, almost monochromatic color of the males. (K.Ch.)

Table 27. Dynamics of catch during 1943 to 1953 (Lockley, 1954)

Years	Catch	
	Average per year (number of animals)	Maximum and minimum per year
1943-1945	940	1,345; 625
1946-1949	710	783; 615
1950-1952	528	707; 397
1953-1954	246	290; 203



Fig. 198. Semiadult gray seal. Northern spits in the White Sea, September, 1970
(photograph by A.G. Beloborodov).

Economic Importance

The gray seal commands little economic importance in our animal hunting activities. Its reserves in our waters are insignificant and hence there are no special hunting prospects here. Before the Patriotic War, its kill in Murman did not exceed several dozens (mainly young animals) per year. To increase the population to a level capable of supporting profitable hunting, hunting should be banned everywhere for 10 years and then a thorough study of its ecology done, especially of its feeding habits, to determine whether this seal damages the salmon population.¹²⁵ If such damage should prove negligible, the gray seal could become a regular source of small numbers of valuable fur. The other ancillary products that could be utilized are the fat (a weaned juvenile can yield about 20 kg of fat and an adult 50 kg or more) and edible meat for animal farms (10 to 12 kg from a young animal and roughly 50 kg or more from an adult seal).

In the Gulf of Finland in the Leningrad region there is neither special hunting of this seal nor is it pursued as a sport. On the Estonian coasts in the prewar years, seals were caught fairly regularly but the gray

¹²⁵ The available general references indicate that in Murman this seal causes no significant damage to the fishing industry.

371 seal was not a frequent catch. Outside the USSR, in the Baltic Sea, the gray seal was caught mainly in the winter-spring in the region of the Åland Islands and the adjoining expanses in the zone of ice fringes and drifting ice floes, in the Baltic Sea itself, the gulfs of Finland and Bothnia, and in smaller numbers, on occasion, in summer and autumn at various other places. The total catch by Sweden and Finland (encouraged by monetary rewards) in the 1940s and 1950s reached an average of 1,000 or slightly more per annum (Table 28).

Outside the Baltic Sea, the killing of these seals is rewarded on the Faeroe Islands (some 800 animals including 500 pups were killed in two-and-a-half years) and in Canada. Great Britain has imposed a prolonged seasonal ban during the breeding and suckling periods.

Hunting in the Baltic Sea is mainly undertaken by fishing vessels cruising in the period of whelping and molting of seals along the fringes and among fairly thin ice floes. Most of the catch there at this time is of the young; quite a few suckling mothers are also caught. Sweden and Finland have no rules whatsoever pertaining to sealing, nor are there any agreements between them regarding it. In the summer-autumn months stray seals close to the coast are killed quite often from launches and boats.

Lack of supervision and totally unrestrained killing of the Baltic gray seal population has arisen because of the commonly held belief that this animal is a plunderer of fish. Without doubt, the gray seal does consume fish. But the fish consumed by it is nowhere, and never has been, of much economic importance and its rapacity is not significantly reflected in the fish reserves and hardly so in the catch. No perceptible damage caused by this seal has been recorded either in Murman or the Gulf of Finland. It has been said that it does not generally damage the fishing industry in the Baltic and North Seas (Freund, 1933) although it was earlier blamed as the most dangerous of seals in the Baltic Sea (Iort and Knipovich, 1907*). Furthermore, it has played no perceptible role as a destroyer of economic fish in some Canadian regions (Mansfield, 1966) despite an increase in its population through controls imposed along the lines of experience gained in Great Britain.

371 **Table 28. Number of gray seals caught in the Baltic Sea from 1930-1959**
(Curry-Lindahl, 1965)

Years	Caught in			Sweden	Total
	Finland				
	Adults	Pups	Total		
1930 - 1939	8,995	17,265	26,260	11,952	38,212
1940 - 1949	3,800	2,715	6,515	6,792	13,307
1950 - 1959	3,743	2,743	6,465	3,597	10,062

Nevertheless, the presence of gray seals is undesirable in the larger economic fishing areas, especially in the estuarine sections of seas through which salmon pass into rivers to spawning sites and back. Here their adverse role on the fishing industry is obvious and controls necessitated. The damage caused by the seals to man is not restricted to the consumption of economic fish, i.e., to the adverse effect on fish reserves, but is also manifest in their consumption or partial damage of fish caught in nets, especially salmon, and the damage they do to the nets *per se*.

In the coastal waters of England and Scotland the damage caused by gray seals is quite significant at places. According to rough but well-argued calculations, gray seals (about 47 head) in 1957 could have consumed roughly 10 tons of true salmon and sea trout in the estuary of the Thames River during the entire fishing season covering 182 days. The damage extending to other fish (cod) as well as squids would account
372 for about 3% of the total catch of salmon (the calculations assumed the following daily ration: adult seals 6.8 kg; immature seals aged two to five years 5.5 kg; and yearlings 2.3 kg) (Lockie, 1962). The total damage inflicted by the seals to the fishing industry on the Scottish coasts has been put at 67,000 pound sterling per annum (Rae and Shearer, 1965). Fishermen of other countries too (Sweden and the Faeroe Islands) deplore these salmon losses. Nevertheless, there is no unanimous view on this subject. The quantum of damage in some other parts of its range is insignificant (in Norway and along the coasts of the two German states) and the gray seal is a protected animal there. (K.Ch.)

Subfamily of Monk Seals or 8-incisored Seals

Subfamily MONACHINAE Trouessart, 1904¹²⁶

These seals are large in size; their body length with tail along the dorsal surface is not less than 200 cm.

The hind flippers have a fairly deep median notch. The first digit on the fore flippers is the longest and the rest gradually decrease in size toward the fifth; the claws are well developed on the fore flippers but those on the hind flippers are highly reduced and sometimes almost altogether invisible. The nostrils are mainly disposed on the dorsal side

¹²⁶ The present structure of the subfamily was established by Gray (1850) long before Trouessart, but Gray named the subfamily *Stenorhynchinae* from *Stenorhynchus*, already used in the systematics of marine invertebrates. (K.Ch.)

The year 1897 is perhaps more correct as this was the year in which volume I of the *Catalogus* was published. (V.H.)

of the snout. A proboscis on the anterodorsal portion of the snout is lacking. The whiskers are fairly flattened, or smooth, or with slightly wavy edges.

There are two pairs of teats.

The skull is essentially massive, with thick bones, and there is usually a broad gap between the orbits. The maxillaries anterior to the orbits are not swollen (not convex). The zygomatic arches project laterally to different degrees. The preorbital processes are prominent in most cases. The external opening of the bony auditory meatus is simple, without prominent lobes. The nasal aperture is less open upward and its upper posterior edge does not extend beyond the anterior margin of the orbits at the back; in most cases, in fact, the nasal aperture does not reach the orbits (genus *Ommatophoca* is an exception). The intermaxillary processes are usually contiguous with the nasal or almost so.

There are two incisors on each side in the upper and lower jaws. The dental formula is:

$$I \frac{2}{2}, C \frac{1}{1}, P \frac{4}{4}, M \frac{1}{1} = 32.$$

The cheek teeth, except for the first premolar, have two roots.

There are no sharp differences in the size and body build and partly in the coloration between males and females. In general, the body build is similar to that of seals of the subfamily Phocinae. The hair coat among newborns is dark toned.

Biological affinity for a hard substratum differs: the seals of one genus (*Monachus*) form rookeries and reproduce on land and the rest of the genera on ice floes.

The distribution of the subfamily is broken into different sections (Fig. 199). These seals are partly distributed in the Northern hemisphere: one genus (*Monachus*) occurs in the subtropical and tropical belt of the Atlantic and Pacific oceans and the rest in subantarctic and antarctic waters, mainly in the zone of drifting ice floes.

374 Monachinae undoubtedly represent a product of the further development of Phocidae. They deviated from the branch of the 10-incisored seals (Phocinae), lost one each of the upper incisors, and acquired the features of high adaptation to pelagic living. This is manifest particularly in the reduction of claws on the hind flippers, in the large notch on the posterior margin of the latter, in the much sharper reduction in length of the digits of the wrist from the first to the fifth, etc.

The evolution of the subfamily has been traced to the Miocene of western and southeastern Europe by which time the members of this phyletic branch had not only fully evolved, but differed in some respects by an even greater specialization (*Pontophoca*). It is highly probable that

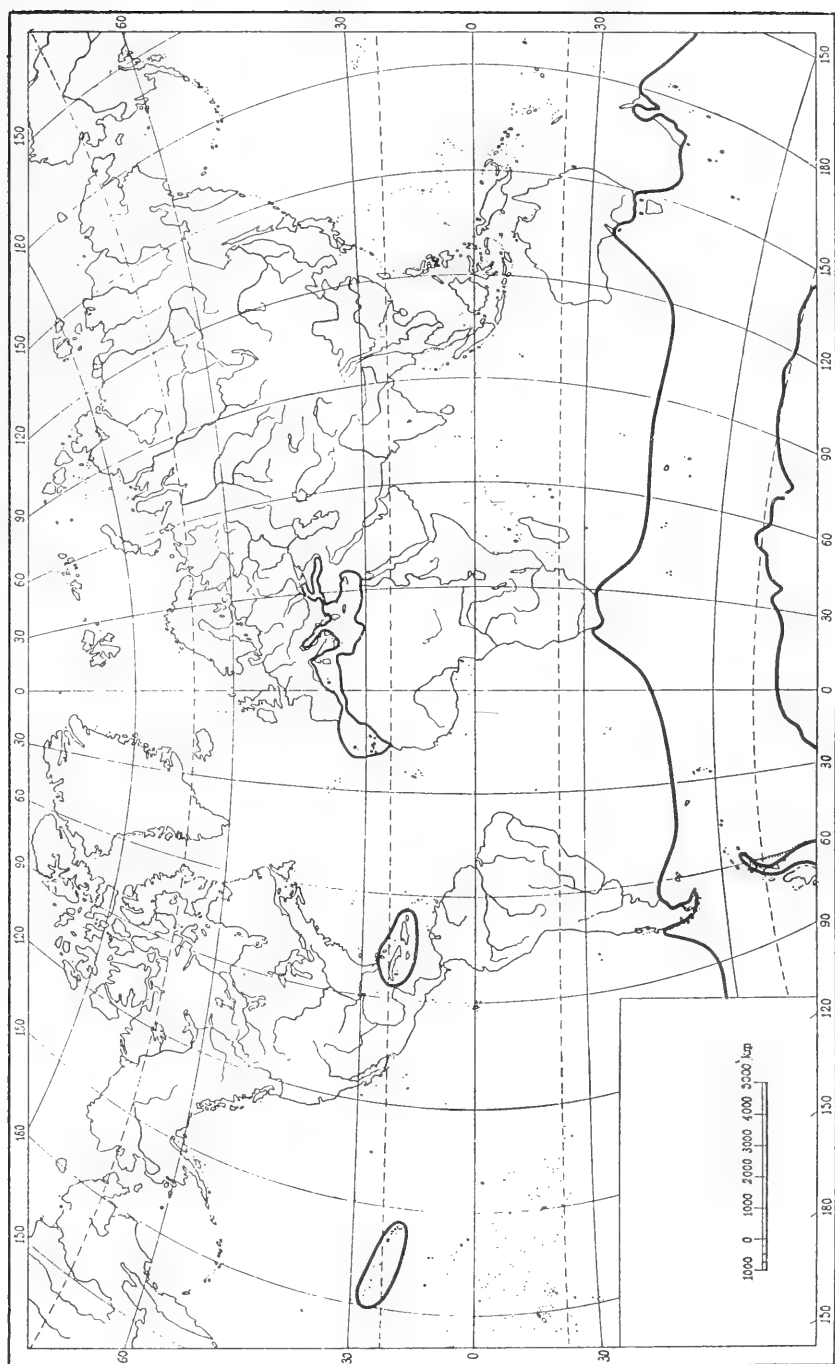


Fig. 199. Distribution of the subfamily of 8-incised seals, Monachinae (K.K. Chapskii).

parts of the Tethys or its tributaries served as the birth place of the primary forms of the subfamily.

The subfamily has not yet been conclusively systematized. Disagreements exist regarding its volume and constituent genera. The old view that the subfamily Monachinae includes only one genus, *Monachus*, is still quite prevalent (Simpson, 1945; and others); the rest of the (antarctic) 8-incisored seals constitute a special subfamily, Lobodontinae Hay, 1930 (= Lobodoninae Kellogg, 1922).

However, it would seem more correct to adopt the structure of the subfamily to include a large volume in the form of a single group combining all the 8-incisored seals (Chapskii, 1961, 1969). At the same time, differentiation of Monachinae at a much lower level, at the rank of tribes Monachini and Lobodontini (Scheffer, 1948*), is entirely reasonable and rational (Chapskii, 1971*). But the spelling should be Lobodontinae.

Insofar as the composition of the genus is concerned, there is every justification (Chapskii, 1969) that it should be left alone in the same manner as adopted at the beginning of this century, i.e., not include the genus *Mirounga* in spite of a recent suggestion to this effect (King, 1966). The subfamily would then contain nine genera (about 41% of all the genera of the family), of which four are extinct and five extant (50% of the contemporary genera of the family): monk seals or white-bellied seals, *Monachus* Flemming, and the four monotypical genera of seals of the Southern hemisphere, i.e., crab-eater seal *Lobodon* Gray; Weddell's seal, *Leptonychotes* Gill; Ross' seal, *Ommatophoca* Gray; and leopard seal, *Hydrurga* Gistel, 1848. The total number of species is seven, which constitutes about 39% of the total number of species of the family.¹²⁷

The species of the subfamily have no economic importance anywhere in the Northern hemisphere because of their negligible population. Until the end of the 1960s, these seals were practically untouched in antarctic waters. The population of some species there, especially of the crab-eater seal, is quite large and the idea of their commercial exploitation is gaining ground.

There is only one genus within the USSR, the monk seal, *Monachus* Flemming, 1822 (20% of the genera of the subfamily), with a single, practically extinct species (roughly 15% of the species of the subfamily).

Encountered in the USSR waters as a very rare, straying single animal. (K.Ch.)

¹²⁷ According to the system adopted in this publication, the family consists of 18 species.

Genus of Monk Seals

Genus *Monachus* Flemming, 1822

1822. *Monachus*. Flemming. Philosophy of Zoology, 11, p. 187. *Phoca monachus* Hermann.
1824. *Pelagios*¹²⁸ F. Cuvier. Mem. Mus. Hist. Nat., 11, p. 196. *Phoca monachus* Hermann.
1841. *Pelagocyon*. Gloger. Gemeinn. Naturgesch., vol. 1, no. 34, p. 163. *Pelagocyon monachus* = *Phoca monachus* Hermann.
375. 1848. *Rigoon*. Gistel. Nat. Thierr. für höh. Schulen, X, p. 32. Renamed *Pelagios* Cuv.
1854. *Heliophoca*. Gray. Ann. Mag. Nat. Hist., 13, p. 201. *Heliophoca atlantica* Gray = *Phoca monachus* Hermann. (V.H.)

Seals of large dimensions. Body length from tip of snout to tip of tail 240-295 cm.

Similar in body proportions to the species of the subfamily Monachinae. There are no sharp external differences between males and females.

The skull is quite massive; the much older animals have fairly intensely projecting zygomatic arches. The sagittal crest is quite distinct though not high; the occipital crests are massive and sharply displaced posteriorly on both sides of the sagittal crest along the linea nuchalis terminalis. The squamose-mastoid processes are very well developed; the posterior margin of the mastoid itself projects slightly posterior to these processes when viewed upward. The nasal processes of the premaxillary bones adjoin the nasal bones. The facial portion (apex) of the nasals does not exceed one-half their total length. The anterior margin of their suture is bisected without forming a median angular projection. The petrosal bone projects into the foramen lacerum posterius.

The upper incisors posteriorly have a prominent transverse groove merging into a frill.

The hair coat is not high but has an extremely prominent nape; the hairs adhere very closely to the skin.

The color of the upper side of the body is a dark gray, blackish-brown, turning very light on the underside. Some sex- and age-related differences exist. The skin around the nostrils and in the gap between them is covered with hair. The whiskers are smooth and oval in cross section. The neonatal coat is dense, quite high and smooth, and very dark. The claws on the fore flippers are well developed but highly reduced on

¹²⁸ Various authors have spelled it differently, viz., *Pelagius*, *Pelagus*, or *Pelagias*.

the hind flippers; nonetheless, their narrow and short tips are visible on the latter.

The seals of this genus are thermophilic and, among all the pinipeds, are the most capable of surviving in subtropical and tropical conditions. They are biologically associated with the coast on which they whelp, suckle the pups, molt, and form rookeries, their size depending on the total population and the nature of the coast. They do not form harems nor do they undertake any significant or regular migrations, being predominantly confined to the coastal zone.

The distribution of the genus is highly interrupted (Fig. 200). Its species are distributed in three isolated regions of the subtropics and tropics of the Northern hemisphere. One is the basin of the Mediterranean Sea (up to the Black Sea inclusive) with the adjoining sections of the eastern Atlantic, in the southwest from Gibraltar to the Canary Islands and the coasts of northwestern Africa. Another is the now practically uninhabited westernmost part of the Atlantic: the Gulf of Mexico and the Caribbean Sea. The third region of distribution is even more isolated, lying in the Pacific Ocean and covering only the archipelago of the Hawaiian Islands.

This genus has evolved through intermediate links from Miocene ancestors found in western and southeastern Europe, including the Sarmatsk formations in USSR territory. A likely direct ancestor of the genus *Monachus* could be some Lower Pliocene form of the genus *Pristiphoca* since a member of the recent genus *Monachus* adjoined the above fossil genus even in the Middle Pliocene. The geological history of this genus binds it to the west of the Old World, especially to the western, southern, and southeastern parts of contemporary Europe, to the basin of the Tertiary Tethys Sea.

377 Paleontological proof and morphological data of the contemporary members of the genus *Monachus* indicate that this genus represents a phyletic base from which other contemporary genetic branches of the subfamily originated and evolved. The genus *Monachus*, more than any other genus of Monachinae, reveals many features relating it to the subfamily Phocinae (especially the petrosal bone projecting into the foramen lacerum, margin of mastoid visible when seen upward, structure of the zygomatic bones, etc.). It may be regarded as a primary element of the eight-incisored phyletic branch originating from the primary Phocinae and serving in turn as a stage for the evolution of its derivative, i.e., the primary ancestral form of subfamily Cystophorinae.

The genus consists of three species, or about 43% of the species of the subfamily: (1) Mediterranean monk seal, *M. monachus* Hermann,

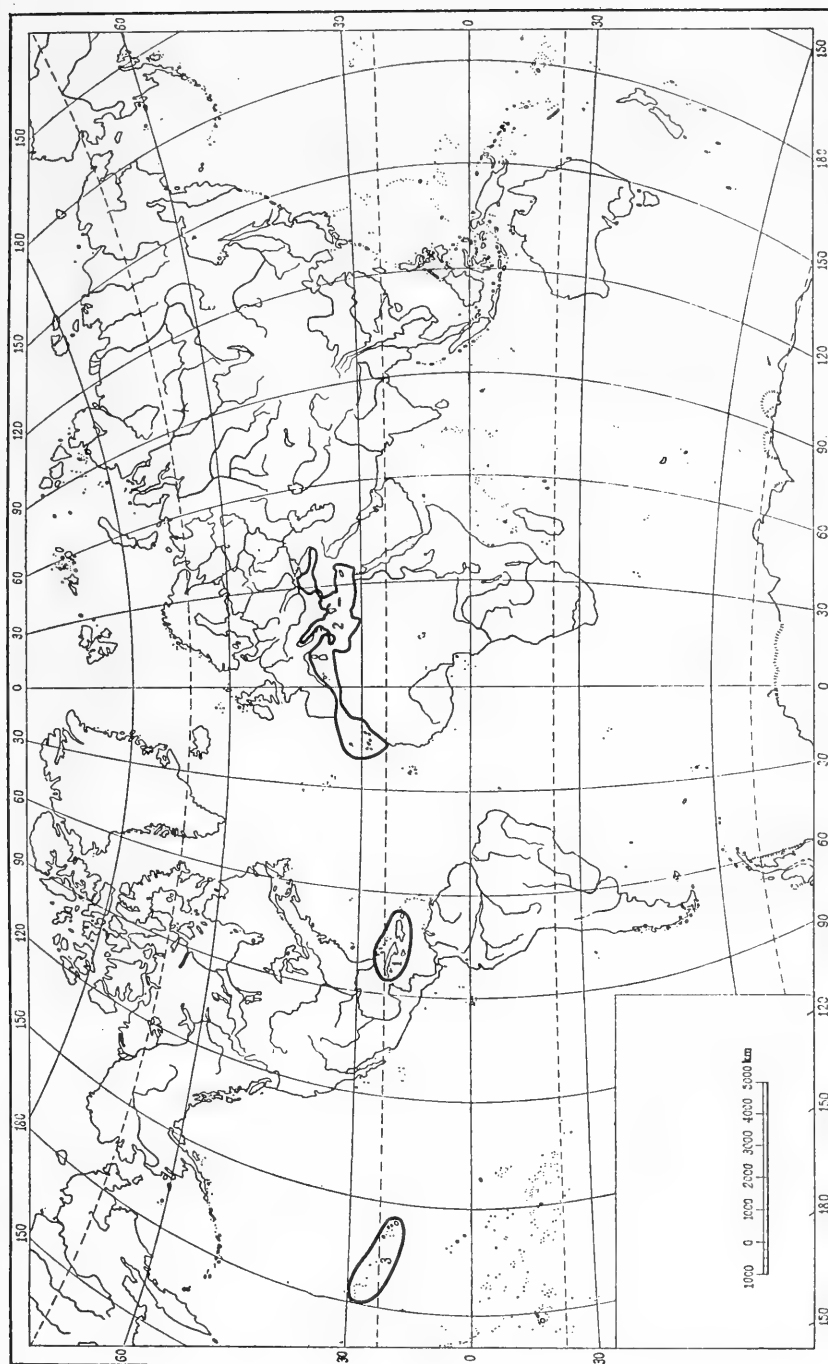


Fig. 200. Reconstructed distribution of the genus of monk seals, *Monachus* (K.K. Chapskii). 1—Caribbean *M. tropicalis*; 2—Mediterranean *M. monachus*; 3—Hawaiian *M. schauinslandi*.

1779; (2) Caribbean monk seal, *M. tropicalis* Gray, 1850; and (3) Hawaiian monk seal, *M. schauinslandi* Matschie, 1905. Though all of these are allopatric, the species characteristics are independent. They differ morphologically in the structure and position of the teeth in the row, in the form of nasal and zygomatic bones, and in other respects. Thus there are two Atlantic and one Pacific species. At present, practically speaking, there are two species (both the species are protected in most places); the West Indian species is apparently wholly extinct.

The fauna of the USSR contains one species, *M. monachus* Hermann, 1779, or 33% of the species of the genus and roughly 0.3% of the species in the fauna of the USSR.

This species was almost extinct in the territory of the USSR even by the second half of the last century. (K.Ch.)

MONK SEAL

Monachus monachus (Hermann, 1779)

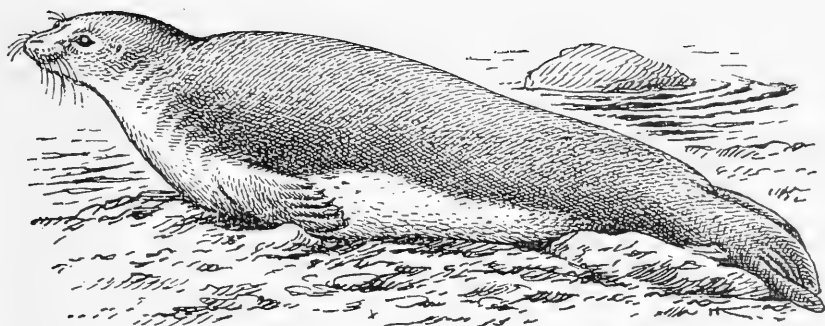
1779. *Phoca monachus*. Hermann. Beschäf. Berlin. Ges. Naturf. Freunde, 4, p. 501, pl. 12, 13. Lake and coast of Dalmatia; Adriatic Sea.
 1785. *Phoca albiventer*. Boddaert. Elench. Anim. 1, p. 170. Adriatic Sea.
 1800. *Phoca bicolor*. Shaw. General Zoology, 1, p. 254. Adriatic Sea.
 1816. *Phoca leucogaster*. Peron and Lesuer. Voyage aux terres Austr. 2, p. 47. Nîmes, southern France, Mediterranean Sea.
 1828. *Phoca hermanni*. Lesson. Dict. Class. d'Hist. Nat., 13, p. 416. Adriatic Sea.
 1838. *Monachus mediterraneus*. Nilsson. K. Svens. Vet. Ak. Handl., 1837, p. 238. Adriatic Islands and Greek archipelago.
 1848. *Phoca crinita*. Menis. Il Mare Adriatica, p. 153. (V.H.)

Diagnosis

The dimensions are large, evidently larger than many other species of the genus. The color is darker. The nasal bones are relatively short and form 16-20% of the condylobasal length. Their anterior margin has a median notch. The upper incisors are disposed in an arc; there is no more than one additional cusp on the premolars posterior to the main cusp. The preorbital processes are well developed. The uncinat processes of the pterygoid bones are not bent angularly outward. (K.Ch.)

Description

In general build, the monk seal does not differ greatly from other seals
 378 of similar size (Fig. 201) but is evidently slightly stockier than many



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Fig. 201. Monk seal, *Monachus monachus* (figure by N. N. Kondakov).

species of the true seals (Phocinae) with a heavier and apparently slightly shortened anterior portion of the body.¹²⁹

The head is flattened on top, as for example among the harp seals (Mohr, 1952). The fore flippers are somewhat shorter than the hind ones. The claw zone on the fore flippers appears as though incised in a strait line while the length of the claws decreases quite uniformly from the first to the fifth digit. The hind flippers have broad terminal lobes due to an angular folding along the inner edge turned toward the apex of the median notch, which is deeper than in the true (10-incisored) seals. The claws on them are highly reduced, very narrow, and barely visible (their length does not exceed 0.5 cm).

The claws on the fore flippers are not pointed but broad.

The hair coat of adults is rigid, smooth, adheres closely to the body, and very low. The hairs are very thin; their length on much of the body is about 0.5 cm (King, 1959*). On the dorsal side of the body of females from Kilii delta of Dunai River, the longest hairs (5.3 mm) were found on the nape, their length on the back and in the tail section being 3.3 and 2.5 mm respectively. The hairs are longer on the belly: the longest of them are in the midportion of the trunk (10.9 mm) and slightly shorter

¹²⁹ This impression is gained from some published photographs (Mohr, 1952; King, 1956; Heck, 1966). It is highly possible that this is due to the jugular section of the male actually appearing in the photographs as massive and comparatively short while the head appears large with a slightly swollen snout. Confirmation of this is the wide spacing of the zygomatic bones in the skull of large males exceeding that in females (see p. 506). Quite possibly, sexual dimorphism does exist among monk seals in the size of the body and the dimensions of the skull, although no direct evidence is available (see p. 506). However, the suggestion that the head of this species is unusually large and resembles that of a bear (Sal'nikov, 1967) is evidently due to a misunderstanding and is explained as due to the poor preparation of a stuffed animal.

on the fore portion (10.5 mm). The hairs are the shortest in the tail section (3.1 mm). The thickness of the hairs is identical in all sections of the body (0.1 mm) (Sal'nikov, 1959).¹³⁰

The neonatal pelage is at least three times longer, incomparably denser, and altogether without nape. It consists of soft, thin hairs.

The labial whiskers are set in five or six rows; their number in a row on each side of the lip decreases gradually from eight to two as the number of the row increases. There is one more lone whisker on top. The total number of whiskers goes up to 70. Their length varies in relation to the position of the row as also the height of the row and probably depending on age and even season (assuming that the whiskers are sloughed during molt). Among the young (less than two years of age) their length varies from 2 to 15 cm. They are oval in cross section, without wavy edges and highly tapered toward the apex. There are hairs like whiskers even in the chin region, their length not exceeding 2 to 3 cm.¹³¹

Supraorbital whiskers do exist, contrary to the opinion of some authors, even among the young animals (not less than three).

The color¹³² of the hair coat of the adult animals is dull and quite often monochromatic. The characteristic predominant shades are gray, brown, and black, as also contaminated tones; the dark color is intensified on the dorsal side of the body compared with the ventral. There is something like a color bloom, creating a faint, bright white or yellowish hue, due to the alternation of light-colored tips of the hairs with compact dark hairs.¹³³

The upper side of the body of adult males is usually a vivid dark gray or slate-black with an admixture of fairly distinct brown shades. On the body flanks, the color turns pale and imperceptibly transits into an even lighter but still vivid gray on the lower side of the body. In this

¹³⁰ According to some other sources (Schapp, Helwing, and Chizelea, 1962), the length of the hairs among the much younger animals varies from 4 to 7 mm on the ventral side of the body.

¹³¹ The description was based on the data of King (1956), Sal'nikov (1959), and Schapp, Helwing, and Chizelea (1962).

¹³² Description of the color features of the hair coat is very difficult because of the extremely few specimens. The number of skins in our museums is very small and such altogether absent for the other species of the genus. Further, due to prolonged storage, the skins have acquired a fairly distinct yellowish-golden hue.

¹³³ There is one more widely prevalent type of coloration in the form of fine light-colored bands or variegations, quite abundantly dispersed in large patches at different places on the body. These are concentrated most often under the chin, along the flanks, and at the center of the neck, and at various places on the chest and back. Since these variegated spots are visible (seen through) on the reverse side of the skin (on the flesh side), they may be regarded as caused by abrasions.

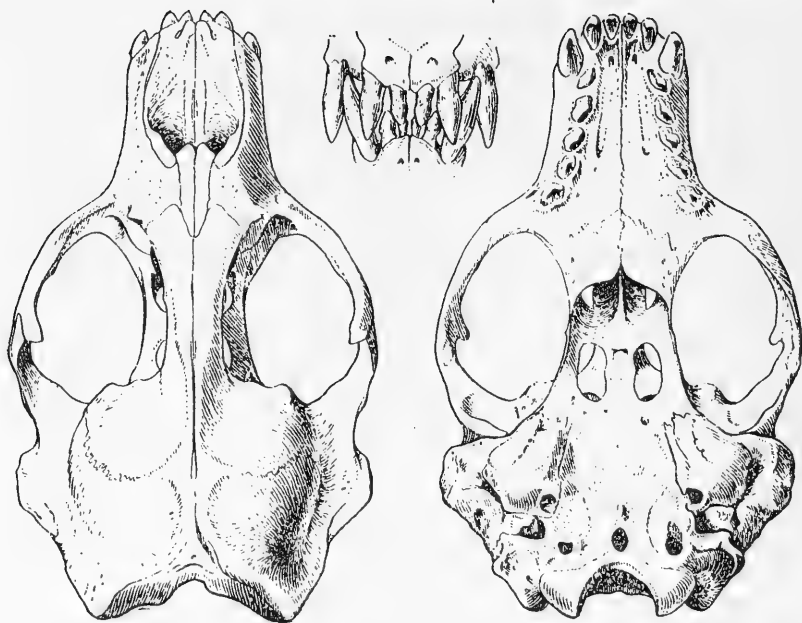
background, a very large spot stands out in contrast. This spot is tens of centimeters across, angular, almost white or slightly creamy, rhomboid or roughly rectangular, and often resembles a butterfly. This is a characteristic feature of an adult male. The spot is usually disposed asymmetrically, most often on the abdomen or on the flanks in the rear half of the body but closer to the fore flippers. Among adult females (King, 1959*; Sal'nikov, 1959), the dorsal side is dark, blackish or dark gray, with a slightly silvery or yellowish bloom due to the light-colored tips of the dark brown hairs. On the flanks, the hair coat gradually turns lighter and becomes light gray on the entire underside of the body, but usually without the large whitish spot characteristic of the males. The yellow bloom often seen on the skins is most likely due to posthumous color changes caused by oxidation of fat remnants present in the skin. The color of the tips of hairs among live animals is mostly whitish or very pale gray, if not white.

The pelage of the newborn is a fairly uniform dark brown or dark cinnamon on the dorsal surface; it turns lighter on the flanks and apparently is even lighter in color on the ventral side.

Evidently, depending on whether the animal is a male or female, on the underside of the body or on the flanks, posterior to the fore flippers, there is, or is not, a large angular spot of white or almost white color similar to that described in the case of adult males. As the neonatal (juvenile) coat is shed, a rigid, very short hair coat closely adhering to the skin is seen; this coat is an altogether different color and is characterized by sharp dichromatism: dark gray on the dorsal side and very light or almost pure white on the ventral side (or ventral side with yellowish tinge). It may be sharply set off on the flanks, roughly at the level of the base of the fore flippers from the dark gray with brown bloom of the dorsal side (Schapp, Helwing, and Chizelea, 1962). Apparently, at this early age, the color of the first definitive hair coat is identical among males and females.

The color of the males of transitional age is highly similar to that of adult animals of the same sex. The former, however, lack the large light-colored spots of the type described above which are characteristic of the adult (and possibly the newborn) males (King, 1959*; Kümerlöwe, 1966*).

The skull is somewhat larger than in the other species of the genus (Fig. 202). Its upper contour when seen in profile usually descends quite steeply toward the fore end roughly from the apex of the nasal bones. The narrow and long zygomatic bones have an anteroventral angular margin distinctly restricted outwardly along the suture. Preorbital processes are distinctly manifest in the form of a nipple. The nasal bones



380 Fig. 202. Skull of monk seal, *Monachus monachus* (figure by N.N. Kondakov).

are anteriorly bifurcated by a median angular notch; the anterior end of each of them is in the form of an angular or tonguelike prominence. The frontal-maxillary suture from the nasal bone to the flexure in the orbit is not shorter than the nasal-maxillary suture and is usually longer. The bony tympanic bullae are roughly triangular, of irregular form, highly elongated forward, lean somewhat toward each other, and terminate considerably anterior to the crest of the articular fossa. Their internal margin is concave with the aboral carotid fossa at their very end. The fontanelles in the choanal region are very large. The posterior margin of the bony palate is in the form of an arc with a notch, often asymmetrical.

The condylobasal length of the skull of adult males is 280-302 mm, of adult females 260-280 mm. The zygomatic width in adult males is 190-215 mm, in adult females 160-180 mm.

381 The teeth are very massive. All the lower premolars and at least two upper ones are set aslant relative to the tooth row. Their crowns are formed mainly with a single massive main cusp at the base of which is a broad fringe (cingulum) from inside. Anterior or posterior to the base of the main cusp or on both sides of it, quite often an additional denticle, barely raised above the cingulum, appears. All the teeth, except the first premolar, have two roots. The upper incisors are disposed arcuately: the

median less large ones are shifted forward slightly compared with the extreme ones. A semicircular notch and fringe in the form of a cingulum is seen on the posterior side of all the upper incisors.

The body length of adult males from tip of nose to tip of tail varies from 210-250 cm; some very large animals could be of much larger proportions. Nevertheless, the figure of 300 cm and above cited in the literature (N. Smirnov, 1929; and others) is hardly reliable.¹³⁴

The adult females are probably somewhat smaller although a gestating female caught on the coasts of Corsica measured 278 cm (evidently up to the tip of the flippers) (Troitzky, 1953). The length of a female from the Kili River bed of Dunai (if not sexually mature, quite close to being so) measured 227 cm (Sal'nikov, 1959). The total body weight of adult animals goes up to 300 kg and may even exceed it. (K.Ch.)

Taxonomy

The monk seal although undoubtedly representing the ancestor from which other species of the genus have evolved, is more specialized in some respects than its descendants. This is manifest in the intensification of the dental apparatus (premolars and molars more massive with a more sharply manifest tendency to a transverse setting, i.e., to the displacement of their anterior edge inward), in the intensification of the maxillary musculature manifest in a broadening of the coronoid process and the lower posterior subcondylar portion of the lower jaw. The enlargement of the zygomatic arches is more significant than among the other species; the transformation of the bony tympanic bullae has proceeded farther, more forward advanced, etc.

The phyletic relations of the monk seal with the other species, in a morphological context agree with the probable direction of the dispersal of the species of the genus: the Caribbean seal is closest to the European seal in the structural features of the skull while the Hawaiian seal differs most. The two former species are related particularly in the steep curvature of the upper line of the profile and generally the greater height of the skull, the greater mass and tapering disposition of the cheek teeth, enlarged subcondylar portion of the lower jaw, structure of the anterior region, general shortening of the zygomatic bones, and structural features of the bony tympanic bullae. On the other hand, the Caribbean seal can be considered closer to the Hawaiian seal in the proportions of the skull (low index of its width) and in some plastic features (length of

¹³⁴ The body length of adult males as established from the published literature, makes no claim on adequate accuracy since not a single author has specified the method of measurement.

the nasal bones and their contact with the premaxillaries, structure of the coronoid process, pterygoid bones, contours of the suborbital apertures, etc.). Some craniological features among the Caribbean seals are of an intermediate character (reduction of the preorbital processes, form of the anterior margin of the nasal bones, length of the zygomatic bones, etc.) (King, 1959*).¹³⁵

The following general features can be cited:

1. The Mediterranean monk seal, *M. monachus*, represents a special species. Some structural features which are of a more primary (primitive) nature are characteristic of it (arcuate setting of the upper incisors, upper
382 contour of skull profile steeply dipping forward, presence of sharp pre-orbital processes, etc.), proximating it to the 10-incisored seals (angular form of the lower anterior margin of the zygomatic bones).

2. Of the other two species, the Caribbean seal, *M. tropicalis*, is more related to it than the other species, while possessing several features bringing it closer to the Hawaiian *M. schauinslandi*.

3. *M. schauinslandi* combines in itself craniological features of a more primitive character (bony tympanic bullae and some swelling of the pre-orbital zone of the rostrum) as also features that are more evolved (long, arcuate zygomatic bones that are concave anteriorly and smoother upper line of the profile). (K.Ch.)

Geographic Distribution

Coastal waters of the Mediterranean Sea along the continental coasts of Europe and Africa and also the coastal islands, including those away from the mainland. Parts of the Atlantic Ocean southwest of Gibraltar up to the Madeira and Canary islands inclusive, mainland coasts of Africa in the south up to 20 to 15° N lat. (Cape Cabo Blanco in the Senegal River estuary), western, Balkan, and southern Asia Minor coastal zones of the Black Sea (Fig. 203).

Geographic Range in the USSR

Forms a negligibly small portion of the northeastern rim of the range.

The reconstructed boundaries of distribution in the last century or earlier covered the western strip of the Black Sea adjoining Romania within the southern part of the coast of former Bessarabia with the region of Zmeinyy Island (Krotov, 1952), the sea along the western coast of

¹³⁵ When evaluating these features, it should be remembered that the data for all the species are extremely scant and the extent of individual variation of several features is not known. All these could be a source of error.

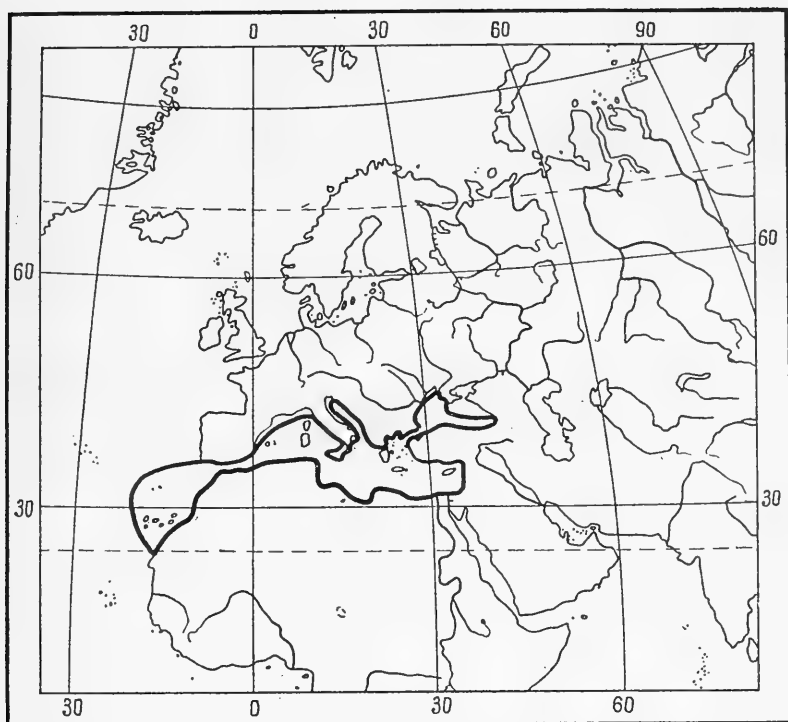


Fig. 203. Reconstructed distribution of the monk seal, *Monachus monachus* in the USSR (K.K. Chapskii).

Crimea, possibly both sides of the Tarkhankut Peninsula (Zernov, 1913), and farther south and east of the southern coast of Crimea from Cape Kherson roughly to Gurzuf (Nordman, 1840; K ppen, 1883*; Puzanov, 1929). Some small tongues of distribution intrude from the side of Asia Minor waters into the extreme southeastern part of the Black Sea toward Batumi (Sal'nikov, 1959). In the early 1840s, these seals were encountered quite often on Zmeinyi Island (Nordman, 1840; Puzanov, 1969*).

Reports on the habitats of monk seals in the region of Sevastopol go back to ancient times although they indicate that seal sightings were generally rare. At the end of the eighteenth century, it was likewise reported that seals were "rarely seen on the coasts including Sevastopol harbor, unlike at other places where they are often sighted" (Gablitsl', 1785*).¹³⁶

¹³⁶ Interestingly, Pallas (1811*), who lived for quite sometime in Crimea at the beginning of the last century, reported that seals in the Black Sea came only from the Mediterranean
contd. . .

The presence of these seals on the southern coasts of Crimea in the first half of the nineteenth century was more accurately reported by Nordman (1840) who indicated sightings in the caves on the rocky southwestern coast. The seals were few, however, and occasionally became targets for hunters. It is interesting that all the recent published reports on this animal are usually a repetition of the earlier publications. Reports of original finds of these seals are extremely rare. Thus, in the 1830s, one seal was killed between Kuchuk-Lambat and Karabakh (Këppen, 1883*) and, in 1834, a very large seal was "sighted on a cape at the end of the land in a botanical garden" (A. Nikol'skii, 1891).

At present, the monk seal lives or reproduces nowhere in the western part of the Black Sea. The appearance of stray animals in the extreme northern portions of the Dunai delta represent extremely rare instances of transgression far beyond the limits of the habitats that are normal for our time. Such instances were noted at the end of the 1930s and early 1940s at some points in the Kilii delta: on Siberian spits, in the narrow straits of Prorva where seals were caught in fishing nets, and also at several other places in the water as well as on sand spits, including the small islets Limba and Kuril (Sal'nikov, 1959). From 1946 through 1951, there were five more instances of seals being caught by fishing hooks (Krotov, 1952), including a female on May 20, 1950. Zmeinyy Island too falls in the same coastal section of the northwestern Black Sea but straying of the monk seal onto this island is as rare an event as in the Dunai delta. There is no positive information whatsoever on finds of this seal farther north along the western coast of the Black Sea barring a reference to an "animal like that of a seal" noticed 30 km east of Odessa in 1950 (Kleinenberg, 1956).

There is no positive information on sightings of the monk seal on the Crimean coasts in this century and it may be regarded as totally extinct there (Puzanov, 1929). In Tarkhankut-Bokkaly region (a unique place where it was still considered possible to sight an occasional seal early in the nineteenth century and early in this century), the seals were obviously more numerous in the remote past (Zernov, 1913). There is no truth, however, that seal populations lived and reproduced on the Tarkhankut Peninsula in the last century. Significantly, there are no other references in the literature of that time to the existence of this seal. Yet, there are persistent reports of seal sightings in the region of Medvezhii caves near Sevastopol beyond the Kherson lighthouse, where these seals were even hunted at the end of the last century (Zernov, 1913).

("In Pontum Euxinum adscendit em Mediterraneo"). However, he was simply repeating the widespread belief of the local inhabitants.

There are three references in the literature pertaining to the southern coast of the Caucasus but they do not inspire confidence. One states that on the coasts of Adler region a whole herd of animals "with prominent snout and whiskers" was seen once (Poznanskii, 1880); another concerns Batumi region near which some fishermen killed a seal in water but could not get it out because it drowned (Kleinenberg, 1956). In the 1920s, near the rocks in the region of Cape Zelenyi (close to Batumi), a few seals settled for several years. Over the course of time their number dwindled and the last of the animals was killed in 1933 by a dolphin hunting ship cruising in Chernaya River estuary (Sal'nikov, 1959). The greater inhabitation of the coasts and the absence of appropriate biotopic conditions are adequate reasons for disbelieving the appearance of monk seals on the southern fringes of the Caucasian coast.

Geographic Range outside the USSR

In the past this covered almost the entire coastal strip of the Black Sea along the Balkan Peninsula (from Dunai to Bosfor) and Asia Minor. In the Mediterranean Sea basin the distribution encompassed almost the whole sea coast and the islands except for the long inhabited sections on the southern coast of Europe (most of the French and Italian coasts and many parts of Spain and Greece) and also some sections on the eastern coast and African coast. Outside the Mediterranean Sea, the distribution covered a small section of the Atlantic Ocean along northwestern Africa, in the south up to Cabo Blanco and even the estuary of the Senegal River (15° N lat.) and also included the Madeira and Canary islands.

Even at the beginning of the present century, much of the coastal waters surrounding the southern coasts of Europe fell outside the distribution while the expanses interrupting the distribution along the African and Asia Minor coasts enlarged. In the 1960s, the distribution comprised a few isolated sites of essentially disconnected diminishing populations. Some are protected by the government, especially in Bulgaria, Yugoslavia, and Rio de Oro.

Only stray wandering animals have been sighted, and extremely rarely, on the Romanian coasts. In the first 50 years of this century, only nine cases of monk seals caught in fishing nets in Romanian territorial waters were recorded and the last such catch (in July 1960) after an interval of 12 years (Schapp, Helwing, and Chizelea, 1962).

In Bulgaria there are two zones of reproduction, both with extremely small populations, namely Cape Kaliakra and south of Burgas. The rest of the Black Sea distribution encompasses the coastal belt of Turkey (Anatolia). The boundaries and the nature of distribution of the species there

are not clearly known but the population can be regarded as extremely small and widely scattered, mainly in the western regions.

Outside the Black Sea, there are a few places where some small reproducing colonies still exist and also some regions where these seals are encountered but their population and reproduction have not been established despite their presence being known for 20 to 30 years. Reproducing populations of the Mediterranean Sea are encountered on some islands in the Adriatic Sea along the Dalmatian coast of Yugoslavia, the Lebanon coast, and possibly here and there the Turkish coast; the existence of one or some small colonies in Greek waters and on the Ionian Islands is quite probable; their presence has been established with certitude on the small islands near Tunisia, in the waters of Morocco, southern Sardinia, and Corsica. In addition to the aforementioned sites, some stray seals are sighted from time to time in the Sea of Marmara, in the Dardanelles, along the eastern fringe of the Aegean Sea, in Salonik Bay, on the Rodhos, Kipr, and Kriti islands, in the northeastern corner of the Mediterranean Sea, and on the coasts of Syria and Israel; the presence of monk seals is also probable on the Egyptian and Algerian coasts, on the Baleares, and at other places.

These seals have been reported southwest of Gibraltar in the oceanic part of their distribution in the region of Medeira (Desert Island) and especially in the continental coastal sections of northeastern Africa to the south of Rio de Oro (in the region of Cabo Blanco). The southernmost point on the coast of northwestern Africa for which information is available about the presence of this seal is the estuary of Senegal River (about 15° N lat.). In general, however, the southern boundary of distribution on the Atlantic coast of Africa roughly corresponds to the 20° winter isotherm of water. (K.Ch.)

Geographic Variation

No information whatsoever is available on the morphological features of the local populations. (K.Ch.)

Biology¹³⁷

Population. Right now, it is not appropriate to refer even to the very existence of the monk seal, let alone its population in our territorial waters. In the remote past, however (a century or so ago), as already

¹³⁷ Information on biological aspects is based mainly on foreign sources which, however, are neither abundant nor thorough.

stated before (p. 510), the seals were regarded as quite common on Zmeinyi Island. They were evidently reported in very small numbers on the *southwestern* coast of Crimea including Sevastopol region although, over a century ago, it was stated that seals in the Black Sea were "few and only rarely stray animals reach the northern coast" (Kessler, 1861).

The population is not much on the coasts of Bulgaria and Anatolia of Turkey. In spite of a total ban on hunting and strict conservation for many decades, the population on the Bulgarian coasts has shown no upward trend. Just 20-30 animals have been reported in the region of Cape Kaliakra (Caspers, 1950). The population of the colony south of Burgas does not even exceed half this number. The Bulgarian population is essentially the only source for the dispersal of this seal in the northern part of the western Black Sea including Zmeinyi Island and Crimea. The rarity of the seal on the Romanian coasts has already been commented upon.

It is not possible to draw a picture of the present population of the monk seal on the Turkish coasts of the Black Sea. Some sixty years ago, 3 or 4 seals were encountered on the Anatolian coasts during a 3-week cruise. This gave grounds for the statement that the sighting of this seal on the Anatolian coasts "was not so rare" (Zernov, 1913). Somewhat later, and also during a three-week cruise, "10 to 12 families" were counted on the west coast of Anatolia, at Zonguldak (Caspers, 1950; Mohr, 1952). There is almost no information from Turkey for the 1960s and that available does not provide a complete picture (Mirsaloglu, 1964 from Kümerlöwe, 1966). It is only known that the seals are sighted every year not only on the Mediterranean coasts, but also on the Black Sea coasts and that small colonies probably do exist on the Anatolian coasts as well (Wijngaarden, 1966*). Since, however, no seal conservation measures have been practiced in Turkey in the last half a century, its population has been considerably depleted and at present is hardly more than the Bulgarian population. Had the situation been different, solitary animals would have been sighted in our waters on the Caucasian coast in the last 30-40 years.

The number of Mediterranean populations, not exceeding 20, is extremely small. Their existence is reliable only at three places: 1) island on the Dalmatian coast of Yugoslavia, 2) northern coast of Corsica, and 3) Tunisian islet Galata. Moreover, two populations of indeterminate strength are encountered on the Ionian Islands and south of the Aegean Sea. The existence of colonies on Crete, on the southern coast of Turkey, and also on the coasts of Libya east of Benghazi is doubtful. The largest population of monk seal is found on the Atlantic coast of Africa, south of Rio de Oro, directly around Cabo Blanco, where some 200 animals (or

even more) have been counted (Kusto and Dyuman, 1953; Wijngaarden, 1966*).

The total number of all the populations of monk seal equals less than a thousand. This number is so small that the species is threatened with extermination.

Habitat. Being an aegialoid [littoral] animal, i.e., biologically associated with coasts, the monk seal is confined predominantly to the coastal zone and is not found deep at sea. Since, however, the coasts within the distribution zone have been extensively inhabited for a long time now, the seals have taken to vacant or less populated sites for breeding. These are mainly rocky islands and generally those sections of the mainland coast which are not inhabited by man. Thus in Crimea the rockier and more rugged sections of the southwestern coast are regarded as sites of their habitation. The seals rarely take to open and low beaches. At least the seal colonies known at present are not associated with such biotopes. It is possible, however, that in the past they did live on the vacant and open beaches of Zmeinyi Island but these were probably only temporary rookeries not associated with breeding. The shallowness of the coasts and their low level explain the absence of permanent rookeries on the vacant and low coasts in the narrow straits of Dunai (Sal'nikov, 1959).

At various sites outside our waters, the seals occupy predominantly the uninhabited and less inhabited islands, more rarely the mainland coasts with complex, highly rugged relief, abounding in rock clusters and various types of rocky recesses. They generally select caves and grottoes, especially those with an underwater inlet. In such rock crevices and caves, protected from the direct action of the surf, the animals eagerly take to sandy-pebbly beaches. Similar biotopes with caves and grottoes abound in the Black Sea (on the Bulgarian coasts at Cape Kaliakra and on the Turkish coasts of Anatolia), in the Mediterranean Sea, and also on the ocean coast of northwestern Africa (including Cabo Blanco). In this context, the explanation for the absence of this seal south of Cabo Blanco, i.e., the coast there is low and sandy, is rather intriguing (since not wholly correct) (Bëtger, 1951*).

Food. Almost nothing is known about the food of these seals in the Black Sea waters of our country. The stomach of females caught in Kili, the narrow strait of Dunai, revealed about 3 kg of semidigested remnants of flounder (*Rhombus maeoticus*) (Sal'nikov, 1959). The catch of seals coincided with the en masse approach of this fish to the coasts for spawning. Judging from the massive teeth of the monk seal, one may assume that it specializes in consuming large fish. This has been confirmed by seal food preferences in zoological gardens and the stomach contents of some specimens caught in the Mediterranean Sea. Thus,

on the coasts of Sardinia the stomach of these seals revealed the remnants of wrasses (*Labrus*) and sparid fish (*Dentex*) (Carrucio, 1893; King, 1959*). The seals were noticed playing with large fish measuring about 70 cm in length. They caught them in their mouth after throwing them up in the air, with the head of the fish turned directly into the mouth (Caspers, 1950). It is therefore hardly correct to suppose the food of the monk seal to be large fish, especially such massive and migratory fish as anchovy and sprat; given the sluggishness of the monk seal, catching such large fish would be difficult (Sal'nikov, 1959). On the African coasts, in addition to fish, the seals consume thorny lobsters (*Palinurus*).

- 387 According to fishermen in the region of Cape Kaliakra, a large seal can consume 15–20 kg, with a preference for sturgeons (Caspers, 1950), but this estimate is doubtful. The daily ration of the seals in zoological gardens reached 12 kg (Gavar, 1927*) and they consumed all types of fish, such as whiting, eel, sardine, salmon, etc.

Home range. Under minimal favorable conditions, monk seals are usually confined year round to the same section of the coast in which they breed year after year, i.e., the seals lead a settled mode of life. The dimensions of the selected sections evidently vary depending on such factors as the size of the population, availability of fairly suitable hideouts, food conditions, etc. The actual population regime on Cape Kaliakra conforms to these factors. The boundaries of the occupied coastal sections could only be tentatively established for each of the given populations.

Daily activity and behavior. Almost no observations on the behavioral features of the animals transgressing into our waters have been reported. Data on the behavior of the monk seal outside our country are likewise scant.

The seals are regularly encountered outside their hideouts in the day (Caspers, 1950; and others) but may be found sleeping even on the coast in grottoes when the brightness is not sharp (Troitzky, 1953). Contrarily, they exhibit the same mobility even in darkness (Kümerlöwe, 1966). It may be assumed that there is no strict sequence of sleep (night) and activity (day). They can be regarded as more diurnal than nocturnal animals. In this respect, observations on the behavior of these seals on Cape Kaliakra are of interest. With surprising stereotyped regularity, noticed for hours on August 23, 1941, the seals swimming from the southern side dove roughly 20 m from a rock. Later, they remained submerged for brief intervals, obviously in shallow water, often surfacing in between, at times with the head ducked and only the back showing above the water. It appeared as though the animals were searching the bottom for something. This probably was so, considering that the water around Cape

Kaliakra is exceptionally transparent. Leisurely swimming thus, submerging and surfacing, the animals turned away for some distance from the rocks. They continued the reverse journey in the same manner until they were lost to sight. Nearly eight minutes later they again appeared and repeated the selfsame behavior. Before submerging, the animal raised its body quite high above the water and flexed its forepart so as to assume the required direction at depth. While diving, air was often exhaled even inside the water, which bubbled up in the form of an arc until the head of the animal surfaced. From this arc one could judge beforehand the point of surfacing. On surfacing, the hissing sound of the animal's expiration was often audible (Caspers, 1950).

Monk seals are generally good divers; they usually throw themselves into water from rocks and are somewhat like sea lions in this respect. They first assume an appropriate posture by heaving the chest.

It has been assumed that monk seals are not particularly good swimmers (Sal'nikov, 1953). Some observations on their swimming capabilities from the coast and from ships (Caspers, 1950) do not justify changing this view. Nonetheless, a slowly swimming animal could hardly seize a large fish. Divers with aqualungs could not approach adult monk seals to photograph them (Kümerlöwe, 1966).

388 The relations between individual animals are hardly known but Bulgarian fishermen were witness to scuffles which, in their view, arose when a new animal entered the colony. The reports of fishermen on regular and severe scuffles between adult females sound somewhat strange. Scuffles are accompanied by loud laryngeal cries resembling at times the bellowing of calves, barking, and even the scream of a beaten or bitten dog (Wolf, 1818*; Carrucio, 1893; Caspers, 1950; Morales-Agesino, 1950*). The voice of young seals is generally similar to that of an adult but fainter and less "fervent" (Morales-Agesino, 1950*) while some have a more characteristic voice. A very young specimen caught close to Livorno, uttered the sound "ovaavaavava" in captivity; sometimes something like a sneeze was heard interspersed with an intense dull sound, and at times the animal emitted a bleat or simply a loud scream (Wolf, 1818; after Mohr, 1952). A newborn seal caught near Split gave out laryngeal sounds similar to "oa" (Priemel and Mohr, 1952*).

Observations of the behavior of captive animals have revealed well-developed higher nervous activity. This is manifest in comprehension and great affinity to man, as noted in its ability to respond to his commands to some extent. A very young animal from around Livorno became totally domesticated after a few months and would "kiss" its master while producing a sound similar to belching. On being brought to Nürnberg, it became totally silent (Wolf, 1818; after Mohr, 1952). Another pup,

which had learned to recognize its trainer, would cry out on sighting her (Ber, 1838*).

Seasonal migrations and transgressions. Being generally confined to a single section of the habitat, monk seals do not undertake periodic or distant migrations. At the same time, the transgressions of stray single animals to fairly long distances from the breeding site are widely known although not frequent. Such animals were sighted in almost all parts of the range and even at its very boundaries. The reasons for these transgressions are not known. It is difficult to say for certain whether the seasonal arrival of fish for spawning plays a significant role in this respect in certain regions. Nevertheless, this phenomenon in particular is used to explain the appearance of some animals and their being trapped in fishing nets in Dunai delta (Sal'nikov, 1959). However, transgressions here are extremely rare and reveal no regularity whatsoever. Were they regular migrations, in spite of the extremely small population, the migrating animals would first have been encountered in somewhat larger numbers and more often, and secondly their departure from Kaliakri would have been perceivable. But, far beyond the boundaries of the colony, on Cape Kaliakri, single animals and almost invariably young ones are encountered (Calinescu, 1936). These phenomena can more naturally be explained as cases of transgression.

Reproduction. Very little is known. The period of mating follows the cessation of lactation although it can commence even somewhat earlier and is evidently protracted. Its calendar periods vary for different animals. Most animals evidently mate in the autumn or at the end of summer. The total duration of the embryonic period (from the moment of mating of the female to parturition) has been put at 10 (Caspers, 1950) or 11 (Troitzky, 1953) months. The whelping period falls at the end of summer-autumn. It is July-August for the Bulgarian populations (Caspers, 1950). Much earlier periods have been reported for the Anatolian coast populations of Turkey: a female caught near Zolgundak delivered a pup in a zoological garden at Ankara on May 5, 1962 (Mursaloglu, 1964 from Kümerlöwe, 1966). According to other indirect data (Zernov, 1913), the period of whelping on the coasts of Anatolia is roughly in the second half/end of July. In the Mediterranean Sea the whelping period extends from mid-August through September and even October (Carrucio, 1893; Dathe, 1934; Troitzky, 1953) and on Rio de Oro, even later, possibly around mid-November (Agasino, 1950 from King, 1956). The reference to spring whelping (Postel, 1950*) is evidently not wholly correct.

It is impossible to establish the dimensions of the newborn because of the absence of information on the method of measurement and on age. Pups with a fresh umbilical cord, found in Dalmatia on September

19, 1933, measured roughly 90 cm and weighed 26 kg (Dathe, 1934). A fully mature fetus was removed from the womb of a female killed on September 27, 1947 on the coast of Corsica; it measured 120 cm in length and weighed 17 kg (Troitzky, 1953).

Lactation extends for 6-7 or 7-8 weeks (Caspers, 1950; Troitzky, 1953). The total duration of the reproductive cycle according to some authors (Caspers, 1950) is 12 months and according to others (Troitzky, 1953), about 13 months and hence births are not an annual phenomenon. It is difficult to say which view is more correct but nevertheless it may be assumed that births are an annual feature in most cases.

Growth, development, and molt. Accurate data are not available on postnatal growth and development. Since the length of the smallest pup at the end of December in Rio de Oro measured 150 cm (Morales-Agasiono, 1950*), it may be assumed that the pups add 25-30 cm during lactation. The period of molt of the neonatal hair coat is not known. It is also not known whether the pup remains on the coast throughout lactation or goes into the water. Some young ones with the neonatal coat fully preserved were caught in the sea. Thus, the Russian hydrobiological expedition in mid-August of 1912 caught on the Anatolian coast a pup that was still completely covered in a firm neonatal hair coat. It molted only after a few weeks (Zernov, 1913). In the second case, a newborn pup with a fleshy umbilical cord was caught on the coasts of Dalmatia. Both these cases point to the ability of even extremely young animals to enter water without molting the primary, neonatal coat. It has been pointed out in the literature, however (Troitzky, 1953), that the pup goes into the water for the first time at the end of lactation and possibly molt. The embryonic hair coat is thus sported for not less than 1.5 months.

A newborn in captivity, weighing 26 kg, was bottle-fed for one week with a mixture of half oatmeal and half cow's milk with a small addition of cod liver oil. This mixture was given six or seven times a day. The pup died due to injuries sustained during transport (Dathe, 1934).

The total growth duration before the onset of sexual maturity has not been established. It has been assumed that the monk seal reproduces for the first time at about four years of age (Troitzky, 1953).

Enemies, diseases, parasites, mortality, and population dynamics. Six species of helminths parasitizing the gastrointestinal tract were detected among monk seals (Delyamure, 1955): cestodes *Diphyllbothrium hians*, *D. latum*, *D. lanceolatum*, and *Diplogonoporus tetrapterus*; and nematodes *Contracaecum osculatum* and *Terranova decipiens*.

These seals face no competition with other pinnipeds. Besides man, sharks pose a threat to the juveniles at some places.

Field characteristics. This is a large seal of deep dark monochromatic coloration on the dorsal side and a different coloration on the flanks and belly depending on age and sex. A large light-colored spot in the posterior half of the body is a characteristic feature among pups and adult males. This is the only species of seal in the Mediterranean and Black seas and also on the Atlantic coast of northwestern Africa. (K.Ch.)

Economic Importance

This seal has no economic importance because of its small population. In some countries (Bulgaria, Yugoslavia, and in Rio de Oro), this animal is protected. It needs to be protected throughout the range of its distribution. (K.Ch.)

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Subfamily of Hooded Seals and Elephant Seals, or 6-incisored Seals

Subfamily CYSTOPHORINAE Gray, 1866¹³⁸

These are seals of large and extremely large dimensions. The body length with tail along the dorsal surface (*Lc*) of adults varies from 180 to 500 cm or more, the males being slightly larger and heavier than the females.

The hind flippers are slightly longer than the fore flippers. The first two digits of the fore flippers are longer than the third and subsequent ones. The claws are quite massive. By the time of maturity, the males grow a dermo-muscular, sac- or proboscislike process on the anterior upper portion of the snout joined to the nasal cavity. This is capable of considerable enlargement on being filled with air. There is one pair of teats.

The skull is massive, broad, with a roomy cranium and zygomatic arches markedly protruding laterally; the zygomatic width considerably exceeds the width of the skull between the mastoid processes. The nasal processes of the premaxillae fall far short of reaching the nasal bones. The nasal opening is wide open and its upper and lateral margins extend far backward. The preorbital processes are well developed.

¹³⁸ The independence of the subfamily Cystophorinae has come under dispute quite recently (King, 1966). Considering the controversial nature of this new interpretation of the family Phocidae, however, its existing structure has been retained. The subfamily is represented in our waters by a single species, which is rather a random find. It nonetheless plays a role in our sea hunting activity in the North Atlantic and hence has been described fairly fully here. The species is also of interest because its biology and distribution were studied quite completely only in the last decade; yet although our scientists put considerable effort into its study, still little is known about it. (V.H.)

The incisors in the upper jaw number two and, in the lower jaw, one on each side. The extreme upper lateral incisors are similar to the canines and slightly longer and thicker than the medial ones. At least the first two premolars have a single root and an almost wholly undivided crown. The cheek teeth are relatively small.

Biologically, the species of the subfamily are extremely divergent. Some of them are pagophilic with no association with the land (hooded seal) while others have almost no association with ice floes and reproduce on land (elephant seals). All of them undertake extensive migrations. In the period of reproduction, males are confined mainly to one and the same rookery along with the lactating females and offspring. The pups at birth are not covered with a luxuriant embryonic hair coat of nearly white color, characteristic of the pups of most of the 10-incisored seals (Phocinae), but rather with a short firm hair coat. Some members of the subfamily (hooded seals) live in pairs at the time of mating while others (elephant seals) form harems. The former mate in water and the latter on land. Fairly large cephalopods and fish play an important role in their nutrition. Hooded seals molt far away from their breeding sites. Elephant seals, however, molt in the very same rookeries and with a far more intense scaling of the epidermis, which comes off in large patches.

The distribution is interrupted and bipolar (borealnatal). Some members of the subfamily are distributed in the arctic and subarctic Atlantic (hooded seals) and others (elephant seals) mainly in the Southern hemisphere, predominantly along the edge of Antarctica, and enter only insignificantly into the Northern hemisphere on the western American coasts (Fig. 204).

The origin of the hooded seal dates back to the Miocene. The seals of this branch originated somewhere in the west of the Old World; the earliest known finds of Cystophorinae have been dated to the lowermost Middle Miocene strata of France (Burgundy). The center of origin of the elephant seals is not known with certainty but possibly falls in the north. But there is a view that they evolved from the Antarctic 8-incisored seals (King, 1966) somewhere in the Southern hemisphere. The occurrence of elephant seals north of the equator in the Pacific Ocean, especially along the Californian coast is quite a recent phenomenon, evidently in the most recent stages of the Quaternary period. The route to this place ran apparently from the subantarctic regions along the Chilean coasts and was facilitated by the cold Peruvian currents.

The system of the subfamily in the conventionally accepted form and as adopted here, is simple. It consists of two genera—hooded seals, *Cystophora* Nilsson with one species (see ahead), and elephant seals,

Mirounga Gray with two species: *M. leonine* Linnaeus, 1758 and *M. angustirostris* Gill, 1866. Some suggested radical changes in the structure of the family, concerning also the subfamily Cystophorinae (King, 1966), as mentioned above, cannot yet be accepted.

One genus, *Cystophora*, is distributed in the northern part of the Atlantic Ocean; one species of the second genus, *Mirounga*, in the Antarctic and the cold temperate waters of the Southern hemisphere (*M. leonina*), and the third on the western coasts of North America, somewhat north and south of 30° N lat. (transgressions into the north up to Vancouver). The ranges of the two species of the genus *Mirounga* are distinctly separate.

Both genera are presently of economic importance but more so the hooded seal, which is a preferential target of sea hunters. Many rookeries of elephant seals destroyed in the last century are now being successfully restored by practicing conservation; at places, as in South Georgia, these are being exploited strictly along economic lines.

In the USSR fauna the subfamily is represented by a single genus, the hooded seal, *Cystophora* Nilsson, 1820. But its presence in our waters is not a regular phenomenon (see below).

From the middle of the 1950s, the hooded seal began to play a positive role in the economy of our country, as Soviet hunting ships were able to negotiate the ice floes in the Greenland Sea. (K. Ch.)

Genus of Hooded Seals

Genus *Cystophora* Nilsson, 1820

1820. *Cystophora*. Nilsson. Skand. Fauna. Dägg. Djur., I, p. 382. *Cystophora borealis* Nilsson = *Phoca cristata* Erxleben.

1911. *Cystophoca*. Brass. Aus dem Reiche der Pelze, 668. Substituted for *Cystophora* Nilsson. (V. H.)

These are seals of large dimensions.

The skull of the adults is massive, with thick bones, but relatively short and broad. The cranium is greatly enlarged but nonetheless stunted. In spite of the large volume of the orbits, the interorbital space is quite broad, slightly more than the maximum diameter of the alveolus of the canine.

The features of the bony tympanic bullae viewed from below resemble a trapezium somewhat; the posterior carotid aperture is disposed on their posterior side along the inner margin. The very large and open nasal aperture is highly enlarged in the posterior upper portion and extends posteriorly beyond the anterior margin of the orbits. The entire bony palate is very long and covers more than one-half the total length of the

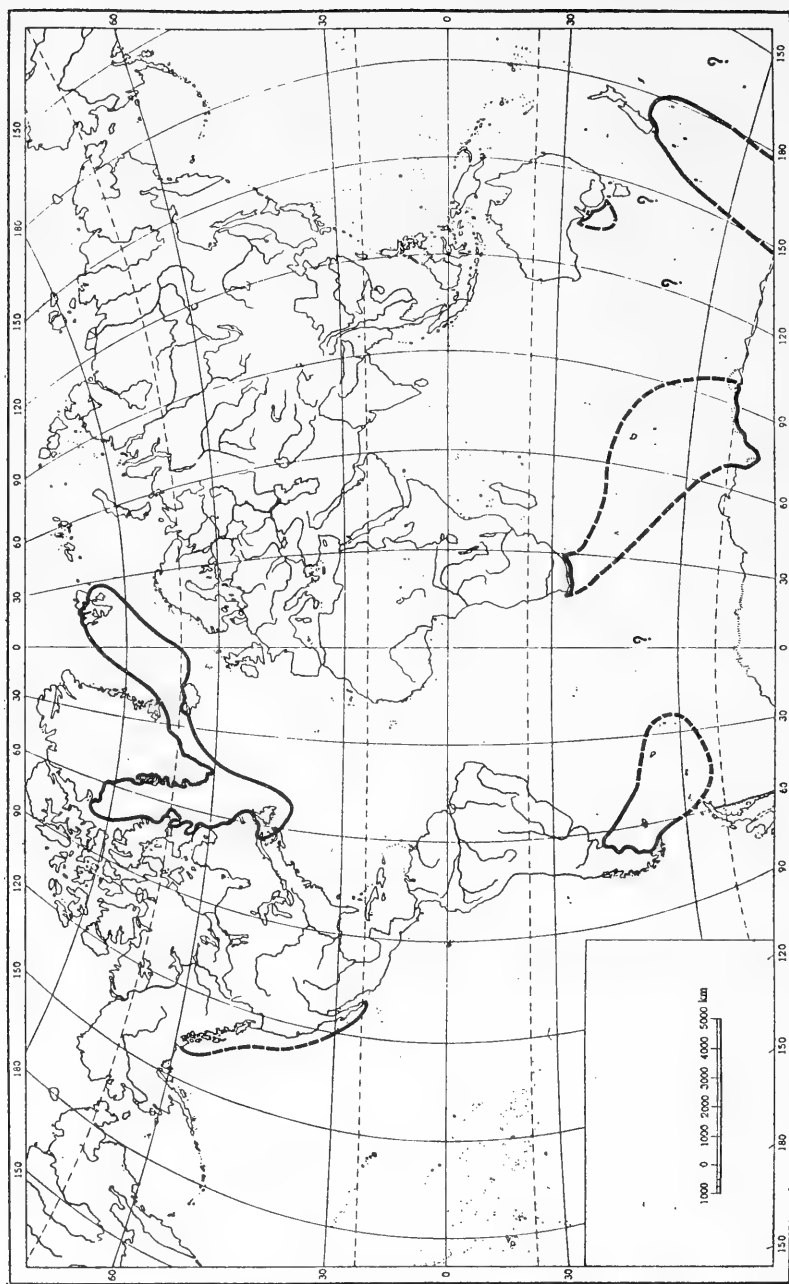


Fig. 204. Distribution of the subfamily of 6-incised seals, Cystophorinae. Broken lines depict the approximate boundaries of distribution of the southern elephant seal, *Mirounga leonina*.

393 skull. The posterior margin of the bony palate is fringed with a wavy line for the most part, like two symmetrical gentle notches converging medially and forming a projection set backward. This projection often has an additional narrower notch/bifurcation in the middle. The palatine bones are elongated and form a very broad bony palate. The choanae are broad and high; their longitudinal bony septum reaches or falls just slightly short of the posterior margin of the bony palate. The length of the zygomatic bones (without processes) is usually not more than double the smallest width. The lower (or posterior) processes are slightly longer than the upper. The maxillary bones are contiguous with the nasals in a small section; their length is usually about one-third that of the nasals and usually less than their width.

The jugular (paroccipital) processes are well developed and bent backward. The nasal bones are considerably advanced forward and are very prominently suspended above the nasal opening. Their anterior portion is fairly enlarged and usually terminates in an obtusely angled median projection (see Fig. 206).

The rostral portion of the skull has no bulges anterior to the orbits and has a concave and not convex (as in 10-incisored Phocinae) profile when viewed from above. The angular process of the lower jaw is weakly manifest.

Cranial sutures not persisting until old age, in addition to occipital (including the lambdoidal) and basal sutures and, in rare cases, even the anterior palatal suture, are characteristic. The dental formula is:

$$I \frac{2}{1}, C \frac{1}{1}, P \frac{4}{4}, M \frac{1}{1}.$$

The canines are very massive; the lateral incisors in the upper jaw are slightly larger than the inner ones and similar to the canines; the molars and premolars are relatively small, with low crowns, slightly flattened from the sides and almost not differentiated. As long as they are not worn out, only a shallow indentation is visible on some as though separating the rear section of the crown in the form of a denticle which, however, may not be present at all. Sometimes, a similar additional denticle is seen in the front. The true molars of the upper and lower jaws have two independent roots. The rear premolars to quite often have two independent or partially used roots.

Adult males are perceptibly larger than females. The claws are well developed on the fore as well as hind flippers. The color of the adults is bright and spotted. The whiskers are horn or brownish in color, flattened, and with wavy edges. On the upper side of the snout from the nostrils to the forehead, the adult males have a hollow dermo-muscular saclike

process formed by an overgrowth of the nasal cavity. At rest, it is barely visible and hangs limply with its fore edge above the tip of the snout. It can be highly inflated during excitation.

These seals are biologically associated with drifting ice floes. They do not form harems. They feed on fish and cephalopod mollusks.

Distributed in the subarctic and arctic Atlantic from Canada to the western parts of the Barents Sea, in some years up to the White Sea inclusive.

These seals undertake distant migrations from the wintering and breeding sites to the regions for molt and feeding. Their main biotope is the marginal strip of drifting sparse pack ice. In the period of feeding they cover even much farther boreal regions to the south.

The origin of the genetic branch has not been traced conclusively with the finds of teeth reported thus far dated to the Middle Miocene formations of France and the Pliocene formations of Belgium. *Mesotaria ambigua*, described from these finds, is regarded as a possible predecessor of the contemporary genus *Cystophora*.

An immediate problem for taxonomists is to provide a more thorough explanation of the morphological differences and similarities between the hooded seal on the one hand, and species of the subfamily of true seals (Phocinae) and the subfamily of monk seals, Monochinae, on the other.

The genus consists of a single species, the hooded seal, *Cystophora cristata* Erxleben, 1777.

This seal is a random find in the USSR where it penetrates into the northern part of the White Sea (its inlet and neck sections).

394 As one of the most important targets of sea hunting, this seal is caught predominantly in the international waters near Jan Mayen, Iceland, Greenland, and Canada for its skin, fat, and other byproducts. (K. Ch.)

HOODED SEAL¹³⁹

Cystophora cristata (Erxleben, 1777)

1777. *Phoca cristata*. Erxleben. Syst. Regn. Anim., I: 590. Southern Greenland and Newfoundland.

1785. *Phoca cucullata*. Boddaert. Elen. Anim., p. 107.

1820. *Cystophora borealis*. Nilsson. Scand. Faun. I: 383. Southern Greenland and Newfoundland.

¹³⁹ This seal is sometimes referred to as the Atlantic gray seal ("tevyak"), which is not correct as this name has been assigned to another species (*Halichoerus grypus*). Hunters sometimes call it the "klappmyss," a word borrowed from the Norwegians.

1824. *Phoca leucopla*.¹⁴⁰ Thienemann. Reise im Norden von Europa, p. 102. Grimsey Island, north of Iceland.
1825. *Phoca mitrata*. G. Cuvier. Oss. foss., 5, p. 210.
1843. *Phoca isidorei*. Lesson. Rev. Zool., p. 256. d'Oleron Island, France. (V.H.)

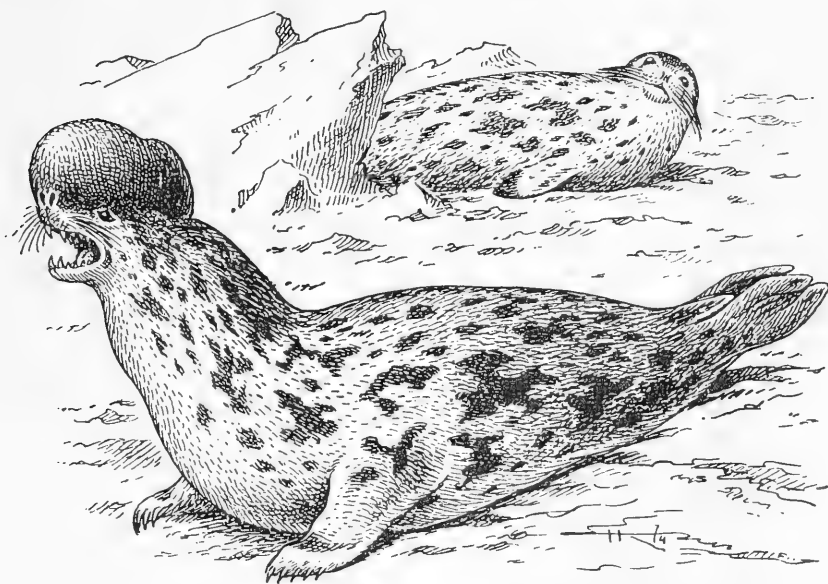
Diagnosis

Only species of the genus.

Description

In general appearance, the hooded seal is similar to the large species of the subfamily of true seals, i.e., common or harp seal, except that it is larger (Fig. 205).

The body is elongated and the fore flippers have a significantly truncated posterior upper margin. The hind flippers do not form a deep recess on maximum expansion.



395 Fig. 205. Hooded seal, *Cystophora cristata*, mature male and female (figure by N.N. Kondakov).

¹⁴⁰ Ellerman and Morrison-Scott (1961*) assign this name to an individual variant of the harp seal. (V. H.)

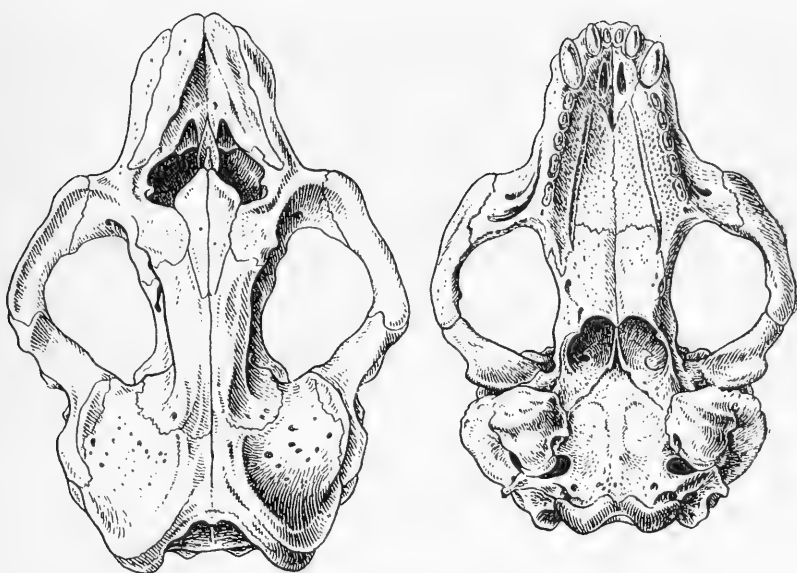
The length of the anterior portion of the body from tip of nose to base of fore flippers is about 31% in females and 34% in males; length of fore flipper in both males and females about 14%, and maximum body girth about 65% of body length (L. Popov, 1960).

Adult males differ sharply from all the other seals of the North Atlantic in having a special saclike formation on the anterior upper part of the head. It represents a spacious paired enlargement of the nasal cavity between the skin cover and skull and nasal cartilage longitudinally divided for the most part by an elastic mucous septum. In the normal (collapsed) state, it is comparatively less recognizable because it is externally bound on the nose bridge by a transverse fold and anteriorly [it] forms a pouch of the rostrum hanging above the mouth opening. When the animal is in a state of excitation, this saclike cavity becomes highly inflated under the pressure of air generated by the closure of the nostrils and stands out prominently above the anterior portion of the snout in the form of a high and thick semicircular balloon with a length up to 30 cm and height up to 25 cm (Fig. 207). In addition to inflating this subcutaneous sac, the males are also capable of blowing a typical
 395 balloon out through either nostril. Such a balloon is formed by inflating with exhaled air the elastic longitudinal mucous membrane separating the saclike cavity.¹⁴¹

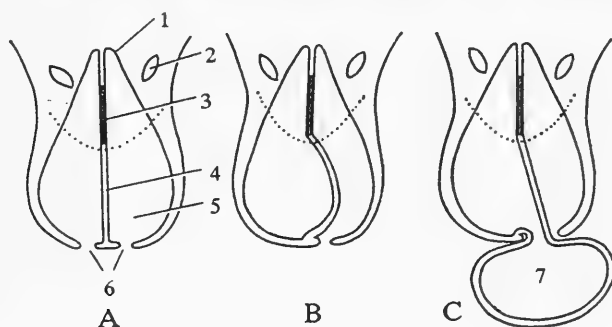
The hair coat of adults is distinctly dichromatic. Dark spots of extremely variable size and shape are scattered quite haphazardly on a light gray background (sometimes darker on the dorsal than ventral side). These spots are slightly angular and quite often of fanciful shapes that frequently merge when the contours are particularly ornate. The spots in the midportion of the body are considerably larger, with more complex outlines, but more sparsely scattered than in the anterior portion, where they become very small close to the head and look like dabs. The spottiness on the dorsal surface is somewhat denser than on the ventral side. The spots are dark brown, often brownish-black or almost black. The anterior portion of the head, hind flippers, and tail are more deeply pigmented and often monochromatically dark. The speckles on the fore flippers are usually quite distinct.

Among males with this type of coloration, much darker animals are sometimes encountered. The spots in them are so large and numerous, especially on the upper part of the body, that there is virtually no space left for the main background; hence such animals appear to be

¹⁴¹ Brondsted, 1931*; Olds, 1950; Trenze, 1950*; Berland, 1958; Mohr, 1958*; Sierts, 1958*; L. Popov, 1960; K.K. Chapskii.



396 Fig. 206. Skull of the hooded seal, *Cystophora cristata* (figure by N.N. Kondakov).



397 Fig. 207. Schematic structure of the nasal cavity of the male hooded seal, *Cystophora cristata*, at rest (A) and in a state of excitation, filled with air in one of the paired chambers (B), causing extension and inflation of the elastic nasal septum (C). 1—posterior portion of the nasal cavity; 2—eye; 3—cartilaginous section of the nasal septum; 4—elastic nasal septum; 5—anterior portion of nasal cavity; 6—nostrils; 7—inflated balloon (after Berland, 1966).

a monochromatic grayish-black from a distance. The females are practically indistinguishable from males in coloration though there are references that the main background among females is lighter and the dark spots more contrasting (Collett, 1911-1912).

The age-related color changes of the skin are significant. The first coat with which the pup is born is characterized by the total absence

of spots and sharp color differences between the ventral and dorsal surfaces. The upper part of the body from the tip of the nose to the tail is a monochromatic bluish-gray with a bluish-olive tinge. This coloration changes sharply on the flanks to almost total white on the lower
 396 side of the body. The color of the inner and lower sides of the flippers is similar. The boundary between the dark and light colors runs from the lower margin of the nostrils 1.5-2 cm below the eyes almost through the ear opening or slightly above it, diverging onto the sides of the [shoulder] blades, and forms a long narrow projection in the mid-portion of the outer surface of the fore flippers. Posterior to them, the boundary extends along the flanks of the body (above the axillae) and reaches, almost without flexure, the hind flippers, terminating in their upper part, and onto the tail.

Such an unusual coloration of pups is seen in the last stages of embryonic growth, a few weeks before birth (Reinhardt, 1865*).

Another characteristic feature of the hair coat of the newborn is that it is not typical of seal pups born on ice floes, i.e., soft, wavy, and very dense; instead the embryonic coat is short, rather dense, and somewhat stiff. This type of coat is seen among other pagophilic seals after the embryonic coat has been shed, i.e., the coat of the newborn corresponds to the second coat of other seals. The embryonic coat is seen in the later stages of fetal growth but is shed in the womb itself sometime before birth. The discarded embryonic hair, in the form of dense matted felt and round disklike clumps, is often detected in the amniotic fluid (Olds, 1950; L. Popov, 1959; Yakovenko, 1959; V.K. Shepeleva). The mechanism of matting of the embryonic hair is not wholly clear but this is hardly due to fetal movements. It is more probable that the sloughed hair is swallowed by the fetus and becomes rolled into clumps during passage through the intestine under the influence of peristalsis and during excretion (Mansfield, 1963). The hair clumps consist of fairly homogeneous light gray hairs, thus revealing the color of the embryonic coat.

The hooded seal is among the largest of the true seals. The body length along the dorsal surface (L_c) of adult males from the Greenland Sea measures 210-250 cm, the largest reaching almost 280 cm; the body length of most adult females is 180-200 cm but some measure almost
 397 227 cm. The average length of males is 235.7 cm, of females almost 195 cm (L.A. Popov, 1959, 1961).¹⁴²

¹⁴² According to Degerbol and Freuchen (1935), the largest males reach a length of 350-400 cm, which is rather doubtful (the method of measuring the length was not specified; it was probably with the hind flippers). According to Mansfield (1963), the average length of males from the western Atlantic is 233.7 cm and that of females 203.2 cm.

The weight of adult males (length along the dorsal surface L_c 225-240 cm) is 260-300 kg; adult females (200-215 cm long), however, weight 145-160 kg (L. Popov, 1959, 1961). The average weight of Canadian-Newfoundland male hooded seals is considered as 317.5 kg (Mansfield, 1963). A large male measuring (L_c) 275 cm long caught on October 31, 1954 on Faeroe Islands weighed 375 kg (Ehlers, Sierts, and Mohr, 1958).

The condylobasal length of the skull in adult males (Fig. 206) varies from 241.5 to 293.0, average 271.5 mm; in females 218.0 to 238.0, average 225.3 mm; zygomatic width in adult males 158.0-223.0 mm, females 155.0-176.0 mm; mastoid width in males 151.0-171.0 mm, females 144.0-156.0 mm; length of upper tooth row in males 58.0-85.0 mm, females 50.0-65.0 mm (L. Popov, 1959, 1961).

The os penis in adult males is 20.5-21.0 cm long, 2.5-2.6 cm wide, 2.0 cm thick, and weighs 32-38 g (Mohr, 1958*). (K. Ch.)

Taxonomy

Only species of the genus.

Geographic Distribution

Predominantly the pelagic regions of cold streams along the southern fringe of the arctic zone and its adjoining northern sections of the boreal strip of the Atlantic.

Geographic Range in the USSR

Only the extreme northeastern branch of distribution extends to the territorial waters of the USSR, not beyond the northern sections of the White Sea covering its inlet and neck sections. Stray hooded seals are sometimes encountered here; family groups are rarer. These are more in the nature of stray transgressions of mothers with pups than regular visits. The hooded seals transgress into these regions possibly together with
398 herds of harp seals migrating to breeding sites. Such instances, though not arising every year, are well known to the White Sea hunters who sometimes sight and catch a few animals while hunting for harp seals.

Geographic Range outside the USSR

The southern distribution of the range passes slightly south of the winter boundary of drifting ice floes from the coastal zone of America in the region of the Gulf of St. Lawrence and Newfoundland Island, encompassing the extensive pelagic expanse to the south and east of the latter and extends (with some bend toward Davis Strait) toward the waters

of southern Greenland. Encircling its southern extremity, it runs farther northeast, covering Denmark Strait, and extends north and northeast and especially east of Iceland through the Greenland Sea and northern part of the Norwegian Sea, then descends close to the Scandinavian Peninsula considerably below the boundary of winter drifting ice floes. Along their fringes and receding from the peninsula to the south, evidently up to the coastal belt, the boundary extends to the southwestern portion of the Barents Sea to the threshold of the White Sea into its northern part. The northern boundary of distribution is the fringe of dense accumulations of perennial arctic pack ice between Spitsbergen and Greenland and evidently the same latitude in the straits between western Greenland and the eastern fringe of the Canadian archipelago (Fig. 208).

Within these limits of the main distribution, the populations of the hooded seal are unevenly distributed. Associated in distribution with the fringes of fairly sparse drifting ice floes, the hooded seals in the course of their annual cycle drift alternately north and south, partly due to the seasonal variations in the position of the ice floe fringes.

The southern boundary of distribution in the winter extends from the southwest, roughly from 45° N lat. at Newfoundland, to the northeast up to the Polar Circle (perhaps slightly south along the Norwegian coasts). In summer, on the contrary, it shifts into a more arctic position,

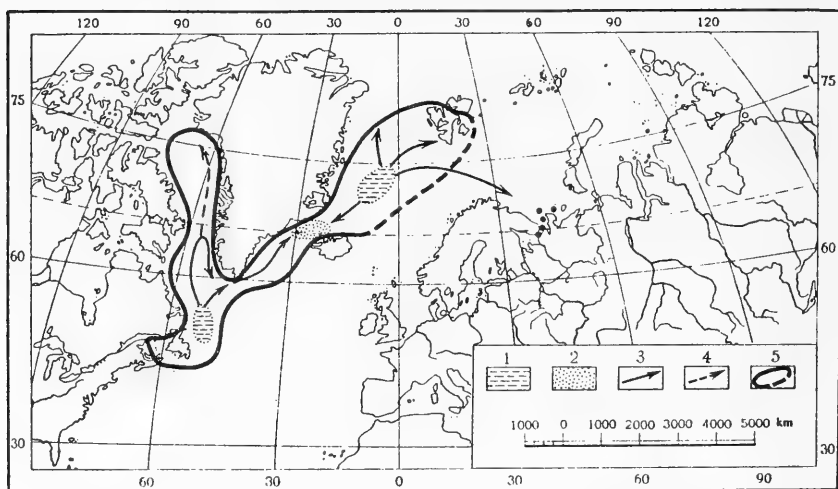


Fig. 208. Distribution of the hooded seal. 1—breeding zone; 2—molting zone; 3—probable courses of migration; 4—including with pups (after Rasmussen, 1960, with additional information); 5—distribution boundaries including probable boundaries (broken line). Dots in the White Sea represent sites of transgression into the USSR waters (K.K. Chapskii).

toward 60° in southern Greenland and Labrador to the Polar Circle in the northeastern regions of Iceland and in the much higher latitudes
 399 toward Spitsbergen and the western part of the Barents Sea. Some populations migrate in the course of the year from some sections of the distribution to others in search of food or sites for breeding, molting, and wintering (see "Seasonal Migrations and Transgressions"). The passive migrations caused by these factors and the active migrations in a relatively short period sharply modify the boundaries of distribution. This reduces the overall zone of distribution into a tentative concept, defined as the maximum distribution range. Thus the distribution is extremely dynamic.

The distribution can be described in greater detail as follows: its western boundary could be drawn along the Atlantic coast of Canada to north of Nova Scotia, encompassing the Gulf of St. Lawrence and the extensive zone of open waters of the Atlantic around Newfoundland, along the coast of Labrador to Hudson Bay, which is intersected by it in the westernmost section, and farther north along the entire coast of Baffin Land with almost the whole Strait of Lancaster and the Admiralty Strait opening into it included. Even more northward, the distribution includes the entire eastern rim of Baffin Land, Smith Strait, Kane Basin, and Robson Bay. This represents the northern limit of distribution between Canada and Greenland. Subsequently, following the coastline of western Greenland, the boundary descends to its southern extremity. Thus Baffin Bay and Davis Strait fall wholly in the distribution. Along the eastern coast of Greenland, the boundary runs from Cape Farewell roughly up to 75° N lat., is separated there from the land usually by broken ice floes, tends northeast up to Spitsbergen, descends along its western side and runs east into the Barents Sea reaching 30° (Nansen, 1924) and even 50° E long. (L.A. Popov, 1960). From this extreme eastern limit, the distribution turns southwest (White Sea) and later, entering the southern boundary traces back in the direction described above.¹⁴³

Since breeding among hooded seals is largely localized, some extension of their spatial division is possible. Apparently, there are three fairly isolated geographic groups, which vary in population and importance. Two of these groups inhabit the western part of the range from the Gulf of St. Lawrence and Labrador to the northern region of Davis Strait and southern Greenland in the east to Denmark Strait. In the breeding period the hooded seals of these groups are concentrated in two regions: on both sides of Newfoundland Island, mostly north and northeast of it,

¹⁴³ In compiling the geographic distribution, the data of Øritsland (1959), Rasmussen (1960), Mansfield (1963), and Øynes (1964) were used.

and to a lesser extent westward in the Gulf of St. Lawrence. The third population is distributed in the northeastern part of the range on the ice floe edges between Denmark Strait and Spitsbergen. Jan Mayen serves as the region of whelping for this group (for more details, see "Seasonal Migrations and Transgressions"). (K.Ch.)

Geographic Variation

Not studied.

Biology

Population. The population of the hooded seal has yet to be precisely determined. At the end of the 1950s, the world reserves were put at 300,000-500,000 (Scheffer, 1958). Aerial surveys were made in 1959 and 400 1960 in Denmark Strait. The total population of the species was put at 500,000 (Øritsland, 1960). Some higher estimates, also assumptions, put it at 500,000-700,000 (Rasmussen, 1960).

The long-term steady hunting in Denmark Strait could serve as a rough index of seal reserves. On average, 62,500 hooded seals were caught there annually from the 1870s. Only a very large herd of hundreds of thousands could have sustained such large catches. Considering this phenomenon, a figure of 500,000 seals was cited even in later years (Chapskii, 1966).

Habitat. Mostly similar to that of the harp seal with which the hooded seal shares much in ecology. Both species are confined to drifting ice floes, mainly to their fringe zones. But while the harp seal prefers comparatively young and low ice floes, the hooded seal selects contrarily very stable perennial pack ice for reproduction. The sites of the hooded seal invariably have frequent waterways since this seal does not make air holes in the ice floe (Nansen, 1924; L. Popov, 1960). As it avoids dense accumulations of ice floes, the hooded seal is not encountered on shore ice. It usually does not enter the deeply protruding bays and straits or narrow straits between islands packed with ice floes. It does not enter deep into the Canadian archipelago, transgressing only into the more southern broad straits opening into Davis Strait and Baffin Bay. For the same reason, it does not approach coasts densely packed with ice floes, remaining confined to their outer fringes.

During the breeding period hooded seals are usually encountered inside the ice massif (which the hunters' schooners cannot always penetrate), on stable arctic pack ice, and around very young ice floes alternating with open water pools. The accumulation of ice floes with open water

pools is particularly characteristic of regions with a slow, often circular drift at the confluence of opposing currents. Jan Mayen constitutes such a region of relatively stable, coarsely and finely broken ice floes. Here, as a result of the interactions between the cold eastern Greenland streams with the northwestern branch of the Gulf Stream, favorable conditions arise for feeding as well as for prolonged residence on the drifting ice floes. The hooded seals find very similar conditions in Denmark Strait, which represents their molting region.

To a much greater extent than the harp seal, the hooded seal is a pelagic inhabitant of open expanses and is seen close to coastlines only in the period of migrations; at this time it prefers the coastal strip of southern, mainly southwestern Greenland. In winter and early spring it is dispersed sparsely in pelagic regions, far from ice fringes, especially in the Norwegian Sea (see "Seasonal Migrations and Transgressions"). In this very period of winter fattening it is also confined to the western Atlantic in the vicinity of the Newfoundland coasts and evidently close to Iceland (Øynes, 1964).

Like other pagophilic seals, the hooded seal requires ice floes for reproduction and molt. This need is also felt when the animals are not fat enough and hence suffer excessive heat loss in water. Ice floes play some role also as a substratum for resting and provide a means of escape from aquatic enemies. The affinity for a strip of ice floes is evidently caused by food conditions, promoted by the polar front zone in general, and the available strip of spring-summer ice floe fringes in particular.

Food. This aspect has not been studied. Only very general references are available regarding specialization of the dental apparatus for grasping and tearing large edible objects including fish (Nansen, 1924; L.A. Popov, 1961). These are essentially the sea perch, flounder, cod, and cephalopod mollusks; the seasonal changes in the distribution of the hooded seal are probably related to the migration of cod. In the
 401 period of suckling pups and even during molt, adults and others in the transitional age group do not obviously cease to feed and go out to sea quite often. Their stomachs revealed food remnants, in particular squids (L.A. Popov, 1959; M.Ya. Yakovenko). Nevertheless, feeding in these periods is very poor and highly irregular. During lactation and molt the animals become quite emaciated (Rasmussen, 1960); intensive feeding occurs after mating, before congregation in the molting region, and also at the end of molt.

On transition to independent feeding, the young seals initially feed on amphipods, small squids, and other edible objects. An adult male in a

zoological garden was fed on herring, whiting (hake), cod, coalfish [pollock], flounder, witch flounder, turbot, and sea perch; this seal refused to eat the latter, however, when a choice was available. Initially, when live fish were fed, it consumed eel, carp, and tench. There was a distinct preference for herring, with up to a hundred consumed daily (Ehlers, Sierts, and Mohr, 1958).

Home range. It is practically impossible to establish the home range of such a widely migrating and wandering animal as the hooded seal. The area of drifting ice floes which the seals select for reproduction is also not amenable to precise calculations, albeit the animals are confined to the same icy regions at this time. Much depends on the actual ice conditions of a given year, type of drifting ice floes, features of approach, and the initial disposition of the animals. Moreover, the density of animal disposition varies even during the short duration of lactation under the influence of ice floe movement.

The animals live in "families" in the regions selected for reproduction. The whelped female is confined to a definite ice floe with her pup; the adult male also stays closeby on the same ice floe, forming a mating pair with the chosen female. Such pairs with suckling pups are disposed at different distances from each other. Generally, each pair occupies a separate ice floe. But when the floe is very large, other pairs occupy it but at distances of tens of meters or sometimes far less. Thus occasionally the hooded seals are so densely disposed at sites of reproduction that the latter resemble the nurseries of harp seals (Rasmussen, 1954*; A.V. Potelov).

In general, however, very uneven distribution of the seals is a characteristic feature during the nursery period. In the large concentration north and northwest of Jan Mayen Island on March 13, 1962, on average five mating pairs with pups were encountered per mile of traverse. On March 24 of the same year, slightly eastward, up to 15 "families" were counted on some ice floes measuring roughly 100×100 m; 15 to 25 animals were sighted from a ship on March 26 on the spits of a coarsely broken ice floe (Khuzin and Potelov, 1963). In general, in the winter-spring season some mating pairs occupy from 670 m^2 to roughly 0.6 km^2 at reproduction sites. Sometimes such mating pairs with pups are typically interspersed among masses of harp seals (R.Sh. Khuzin).

During molt on the ice floes in Denmark Strait the disposition of hooded seals is denser and more stable. The distance between animals is just a few tens and sometimes even a few meters. During local movements and more so during migrations, the concept of "home range" is

no longer applicable due to the wide scattering of the animals and their uninterrupted movements.

402 *Hideouts and shelters.* The hooded seal does not seek hideouts and shelters on the ice floe or in the snow. As a rule, it does not make air holes in the ice floe but utilizes the natural openings and open water pools for emerging onto and exiting from the ice. When, however, the open water pools have a thin ice cover, the seal can pierce it for respiration. In 1956, a hooded seal under observation pierced a young ice cover 4.5 cm thick with its head, thrust up out of the water, surveyed the surroundings, filled its lungs, and submerged never to be seen again. Perhaps the seal managed to breathe at other places in a similar manner as open water was nowhere visible, the entire surface was frozen and calm, and frost prevailed (M.Ya. Yakovenko).

Daily activity and behavior. These aspects have not been studied. During the molting season, the animals rest long periods on the ice floes interspersed with brief spells of submergence in water. Males and females enter water even more often during the period of suckling the pups. The animals spend time predominantly or exclusively in water for the purpose of feeding and moving about.

Seasonal migrations and transgressions. Hooded seals are among the widely migrating seals. Although not much is known about their migrations, their general characteristics have been established. During the breeding season the productive males and mothers are grouped in two widely separated regions. One group concentrates in the southwestern part of the range, on the southern extremity of Labrador opposite the Strait of Belle Isle and the northernmost extremity of Newfoundland. A small population locates in the Gulf of St. Lawrence. The other region occurs on the eastern boundary of the range, northwest of Jan Mayen Island.

The hooded seals reproducing in the westernmost section of the distribution, having completed this biological cycle by early April, abandon the ice floes for sites abounding in food. They first travel along the edges of Labrador north toward Davis Strait and later, turning east, approach the western Greenland coasts rich in fish and feed for sometime right at the banks as also in the coastal regions of southwestern Greenland. Further, some groups of seals move higher and approach Greenland at latitudes 65 to 66° and others (the majority apparently) remain in the feeding grounds, not moving north of 60 to 61° N lat. and are seen roughly at the same time in May on the southern coasts of Greenland.

Having recovered their fat reserves to some extent by the end of May to early June, the hooded seals reach the southernmost tip of Greenland, move round Cape Farewell, and continue their course along

eastern Greenland (instances are known of hooded seals marked near Newfoundland being recovered at Cape Farewell).

Later, the seals migrate farther northeast along the ice edges to Denmark Strait, the main (though not the only) site where hooded seals gather in large numbers and remain for molting in June and July.

In its first year, the juvenile does not undertake this migration eastward; it migrates evidently farther north into Baffin Bay and remains there until August.

Having completed molt, the adult hooded seals begin to leave Denmark Strait in the first half of July and scattering widely, return by the same route to the southern tip of Greenland, and passing it repeat their journey in a reverse direction. Roughly from mid-July through mid-August, hooded seals emaciated during molt are caught on the coasts of southwestern Greenland. Returning to their birth place, the Canadian-Newfoundland population again visits the western Greenland fish banks and feeds well. These seals then pass through Davis Strait and are seen on the Labrador coasts in early autumn, proceeding south into the region of the Great Newfoundland banks for feeding. They return north in February to the whelping zone and concentrate again on ice floes before commencing a new annual cycle.¹⁴⁴

403 The populations reproducing in the region of Jan Mayen Island, after whelping and mating also scatter quite extensively but their migration does not attain the scale that is characteristic of the Canadian-Newfoundland populations. The pups abandoned by their mothers migrate initially passively with the moving ice fringes and are encountered at April end to early May as highly scattered solitary animals in the fringe zones from 69 to 76° N lat. (L.A. Popov, 1960; and others).

From April to June the adults are scattered even more widely among thin ice floes and beyond the fringe zones. They are then capable of distant migrations in search of food. These migrations sometimes extend right up to the White Sea. A large collection of hooded seals, somewhat like a nursery in the Greenland Sea (on Jan Mayen Island), was encountered around May 10, 1962 in the middle of the Barents Sea (73° 38' - 74° 00' N lat. and 24° 28' - 35° 20' E long.) (V.A. Potelov). Much of the population nevertheless tends southwest into Denmark Strait where it molts in June. The rest is scattered on the fringes of the Greenland Sea to north of Jan Mayen roughly up to 75° N lat. and molts there on pack ice (Wolleback, 1907; L. Popov, 1959; R.Sh. Khuzin).

¹⁴⁴ According to Allen (1880), Nansen (1924, 1939), Bartlett (1928*, 1929), Øritsland (1959), Rasmussen (1960), Mansfield (1963), and others.

At the end of the molting period, the Jan Mayen hooded seals are again scattered over an extremely wide expanse whose boundaries were only recently deciphered. It was assumed that they were confined to the high latitudes and appeared near the mainland only very rarely. There were frequent reports from fishermen using nylon nets to catch cod and halibut in the Norwegian Sea, of hooded seals being caught in them at Olesund, northern Tronnølag, Vesteralen region, and other places along the Norwegian coast. Hooded seals were seen there even in winter and were very common in spring. Such instances were particularly numerous in the spring of 1959 (Øynes, 1964). These facts compel us to recognize that, in winter and even in spring, the seals of this species stay regularly at relatively low latitudes not only in pelagic zones, but also close to the coasts, entering even into the Norwegian fjords.

Instances have been recorded of scattered solitary animals at different points on the coasts of Scotland and England; one find has been reported even from Biscay coast of France. In most cases these were young animals, some of which had only just been born. Along the American coast of the Atlantic Ocean south of Nova Scotia, instances have been reported even recently of the appearance of solitary animals in the region of New Jersey and on the coast of Massachusetts; a dead female was found right on the coast of Florida in the winter of 1916 (Miller, 1917*).

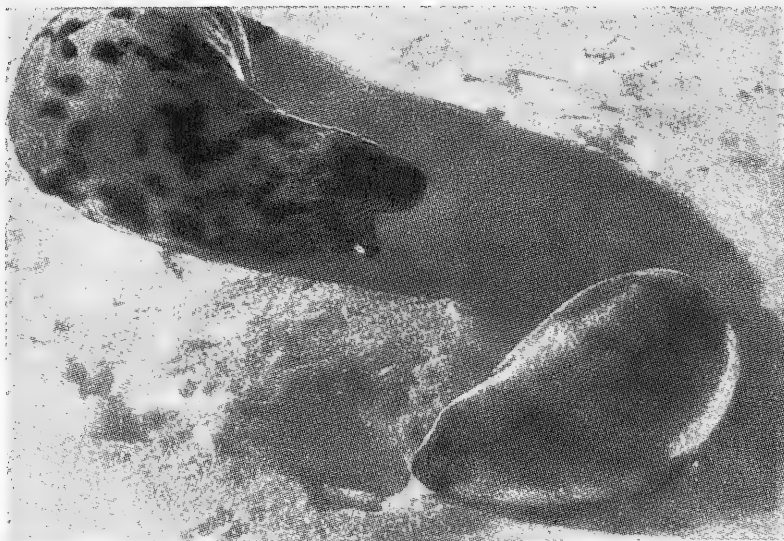
The transgression of a hooded seal into the eastern zone of the Yenisey estuary is wholly exceptional in the matter of distance involved and is inexplicable (N. Smirnov, 1908, 1929).

Reproduction. The period of mating sets in immediately after the completion of lactation and extends roughly for two weeks. Even by around April 10, ovulation has occurred among almost all the mature females; the bulk of the animals mate in the first week of this month (L.A. Popov, 1959; Øritsland, 1964).

Precise information is not available about the copulation process but animals were observed mating in water. The pair slowly floated close to the surface, periodically thrusting out for respiration. The extremely large size of the males, larger than the females, suggests that they woo the females anew each year. Traces of fights in the period of heat have been detected on the skin of males (Yakovenko, 1959).

The lag in implantation of the blastocyst has been established as 3 to 4.5 months from the time of mating, i.e., up to July end to early August (Øritsland, 1959, 1964).

404 The hooded seals whelp in different parts of their range almost simultaneously, in most cases in mid-March; pups appear only very rarely at a much later period.



404 Fig. 209. Pup of hooded seal with mother. Jan Mayen region (photograph by A.V. Yablokov).

Twins have not been reported among the females studied but sometimes two pups have been seen near the same female.

Unlike other seals, sexual maturity among hooded seals sets in relatively early; in rare instances, the first ovulation occurs at the age of two years but in most cases does not result in gestation (Øritsland, 1964; Yakovenko and Khuzin, 1965*). Even at the age of three years, only half of the females are pregnant. Only 80% of the 4-year-old females whelp while 10% of the five-year-olds still remain nonproducers (Øritsland, 1964). Subsequently (most often from seven to eight years), females whelp every year (number of barren animals is not over 5%). The ability to become fertilized and whelp is maintained right up to the end of their lives, which can be taken as 35-36 years.

The onset of sexual maturity among males occurs somewhat later. Until three years of age, they are mostly immature.¹⁴⁵ At four years some males evidently become mature but number about 30%. This rises to 80% among five-year-olds (L. Popov, 1960). Commencing from six years of age, all males are mature (Khuzin and Potelov, 1963) though,

¹⁴⁵ According to Yakovenko (1959), 3-year-old males (with four layers on the cross section of the canine) are already mature and evidently come into heat since the skin of one such animal revealed wounds inflicted in a fight.

according to other authors (L.A. Popov, 1960), immature animals are still encountered at this age, their proportion reaching 13%.

The sex ratio among the newborn is 1:1 as observed from the numerical ratio between the males and females in the molting rookeries. Of 1,125 pups examined, 49.2% were males (Øritsland, 1964).

405 *Growth, development, and molt.* The length of the newborn along the dorsal surface, judging from the size of the fetuses measured in the period of whelping (about mid-March and even in the first few days of April), varies from 79 to 112 cm, on average 100 cm (Collett, 1911-1912; Nansen, 1924¹⁴⁶ L.A. Popov, 1959; Potelov and Yablokov, 1967*; V.A. Potelov).

The newborn weighs 12-27 kg, on average 19.3 kg (V.A. Potelov). Other figures too have been cited (23-30 kg) but the pups were probably already full grown and better fed.¹⁴⁷

After 10-15 days of lactation, pups (Fig. 210) grow to 117 cm (*Lc*) on average while the weight increases up to 37.5 kg on average, the range being 23-55 kg (V.A. Potelov). The fat content of the milk has been reported as 43% (Khuzin and Yablokov, 1963) and on average 60% (with a protein content of 4-9%) (V.A. Potelov).

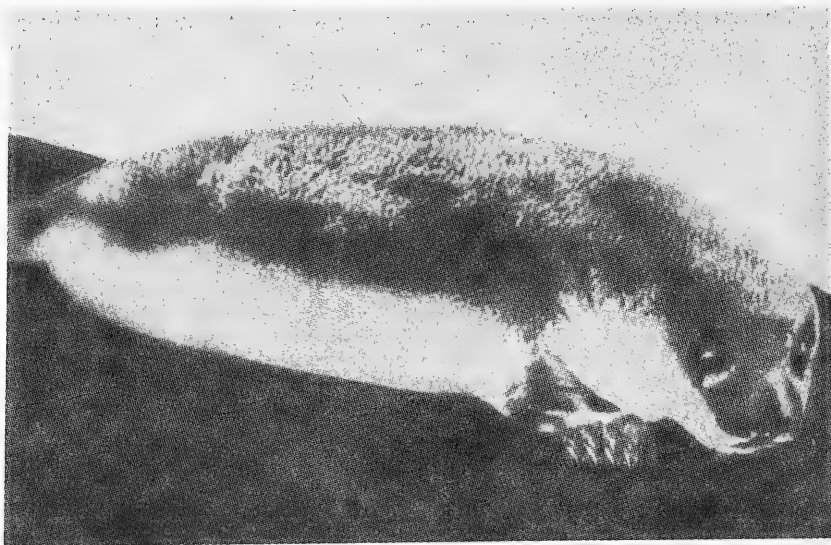
Toward the end of the period of lactation, the thickness of the fat layer in the skin increases to 4-5 cm from 1-1.5 cm at birth (L. Popov, 1961; Shepeleva, 1971); of this, the thickness of the fatty tissue is 3.5-4.0 mm.

The subsequent overall growth of the animal proceeds with the same intensity: the body length of yearlings measured along the dorsal surface (*Lc*) increases to 135-150 cm, up to 160-170 cm at two years, and 170-185 cm at three years of age (Yakovenko, 1959). According to others (Rasmussen, 1960), the body length measured along a straight line (*Lcv*) among yearlings of males and females is identical at an average of 133 cm¹⁴⁸; sex begins to exert a pull in the two-year-olds; the average length of males then is 155 cm, of females 152 cm. At three years of age, the males measure on average up to 172 cm, females up to 164 cm. The same intensity of growth continues up to 10 years of age (when the males grow to an average of up to 218 cm and females up to 193 cm).

¹⁴⁶ Nansen and Collett indicate the length of the newborn as 90 cm. The measurement was evidently along a straight line, i.e., *Lcv*.

¹⁴⁷ The much older data of 3-5 kg (Ognev, 1935) or 6-8 kg (M.P. Vinogradov, 1949) are undoubtedly erroneous.

¹⁴⁸ There is a view that sex-related differences in body length exist even at the time of birth and increase slightly during lactation (Potelov and Yablokov, 1967*) but the data in support of this view are not very convincing.



406 Fig. 210. Pup of hooded seal. Greenland sea (photograph by V.K. Shepeleva).

Growth continues, although at a slower rate, up to at least 20 years of age.

The age-related changes in color of the hair coat reveal some characteristic features. The original, neonatal color remains unchanged for a year. After the first molt (i.e., at the beginning of the second year), the first spots, not yet vividly pigmented, appear on the anterior portion of the back and partly on the neck (Nansen, 1924; Yakovenko, 1959). In the course of a year their number increases and these spots extend over much of the back and are also seen on the chest but not in the belly region. In the first few months of the fourth year (after the third molt), the main background on the upper side of the body turns olive-gray and is covered with the innumerable dark brown spots characteristic of the color of adult animals. The underside of the body also acquires a brownish tinge and is speckled with spots scattered haphazardly. The snout becomes dark. On attaining the age of seven years, the main background turns lighter in color while the spots become darker (Yakovenko, 1959). This skin pattern evidently remains unchanged until the death of the animal. According to some authors, the immature animals of both sexes are distinguished from the adults only in the number of spots, which increase far more with age; the main background, however, remains uniformly light in color (L. Popov, 1959b).

The nasal skin sac is not manifest at all among the newborn males in the first year. In the second year it becomes prominent as a "tiny cushion" slightly enlarging when the animal is excited (L. Popov, 1959b). The sac as such is manifest in the fourth year (Yakovenko, 1959). A real "hood" was seen in a five-year-old male (age established based on marking) (Rasmussen, 1957).

The hooded seal begins to molt three months after the end of the whelping period. Denmark Strait is the main site of congregation of hooded seals of all ages (except under-yearlings) for molting; they gather there from around June 10 and leave toward July 20. Thus the molting period extends for 1.5 months. The molting rookeries of the hooded seal are less dense than those of the harp seal but are far denser than the nurseries of the former. There are no distinct age- or sex-related differences whatsoever among molting hooded seals: the animals are disposed alternately in close proximity. Outside Denmark Strait, no other such region of en masse collection of hooded seals in the molting period is known, but small numbers of molting hooded seals are seen in Jan Mayen and Spitsbergen regions and generally almost all along the fringes of ice floes in the Greenland Sea (Øritsland, 1964; R.Sh. Khuzin).

Enemies, diseases, parasites, mortality, competitors, and population dynamics. The young seal spends its early life on ice floes in an almost sterile icy environment under the protection of adults without exposure to any factor of natural mortality to which this population is sensitive. Later, when the juvenile enters the water and fends for itself on the fringe of ice floes, it may fall prey to the Greenland shark or killer whale. The latter possibly attacks rather frequently even the adult seals. Among other enemies is the polar bear but the hooded seal is much less threatened by this animal than the other arctic seals; furthermore, the population of this predator in the Jan Mayen region is not much. In July, 1956, the stomach of a polar bear killed in the Greenland Sea revealed the remains of a hooded seal pup (M.Ya. Yakovenko).

This seal is parasitized by 15 species and two larval forms of helminths.¹⁴⁹ From among the trematodes, *Metorchis albidus* infects the gall bladder and bile ducts of the liver, *Opisthorchis tenuicollis* and *Pseudamphistomum truncatum* the bile ducts of the liver; from among the cestodes, *Anophryocephalus anophrys* and *Diplogonoporus*

¹⁴⁹ The review of helminths was compiled by scientists of the Department of Zoology of Crimean State University based on the following data: Rudolphi (1819), Siebold (1848*), Brown (1893*), Price (1932), Berland (1963), Skryabin (1950*), Delyamure (1955), Delyamure, A. Skryabin, and Treshchev (1965*), Delyamure, Skryabin, and Alekseev (1964*), Treshchev, Zavaleeva, and Potelov (1967), and others.

tetrapterus infect the duodenum and the small intestine while *Diphyllbothrium latum*, *D. pterocephalum*, *Pyramicocephalus phocarum*, and *Diphyllbothriidae* g. sp. infect only the small intestine; from among the nematodes, *Contracaecum osculatum*, *Terranova decipiens*, *Phocascaris phocae*, *Ph. cystophorae*, and *Anisakidae* g. sp. parasitize the stomach and small intestine while *Skrjabinaria spirocauda* parasitizes the heart, lungs, and blood vessels; from among the acanthocephalans, *Corynosoma strumosum* and *C. semerme* infect only the intestine.

The dissection of 293 hooded seals (Treshchev *et al.*, 1967) established a high rate of infectivity; helminths were detected in 61.4% animals. If, however, the newborn (96 pups) are excluded from the total number of dissected animals and only the adults (197 seals) are taken into consideration, the percentage of infectivity rises to 91.4. The most severely infected seals were aged 1 to 12 years. The most frequently infected organ was the small intestine (in 58.02% animals); less frequently infected were the stomach (29.35%), duodenum (27.9%), and even less the heart (3.4%), lungs (1.02%), and liver (0.68%).

Parasites sometimes cause severe diseases. The nematode *Ph. cystophorae* is capable of perforating the intestinal wall of the host. *S.*



spirocauda, a parasite of the heart, probably kills the hooded seals at six to seven years of age (Delyamure and Treshchev, 1966).

408 The seal louse *Echinophthirius horridus* parasitizes the skin and the seal mite *Halarachne halichoeri* the nasal cavity.

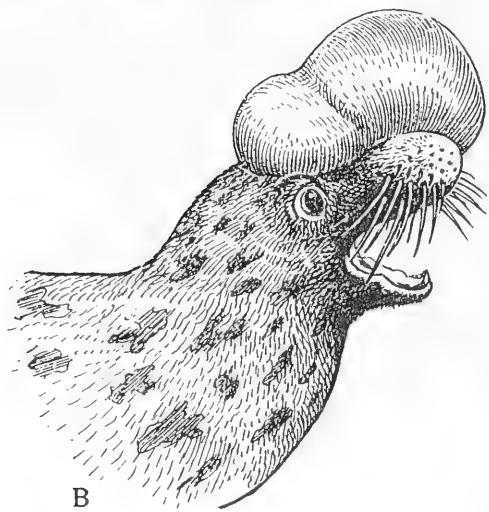
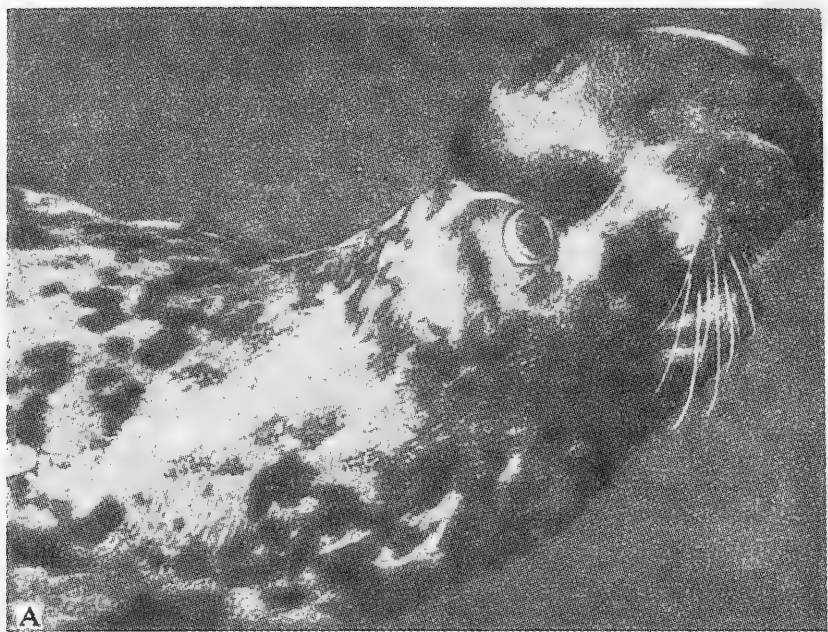
Competition in the feeding grounds can arise only from the harp seal. In practice, however, there is no such competition as the food reserves suffice to meet the needs of both species; furthermore, the hooded seal, more than the harp seal, lives on deep-water nektonic life. Had there been an acute competition, the two species would not probably have formed nurseries in the same regions. Most of the feeding grounds of these two species are nonetheless distinct.

Some idea of the population reduction can be gleaned from hunting statistics, especially a perceptible increase in younger animals in the herd, i.e., a relative reduction in the number of mature animals and an increased percentage of young ones. In 1956, the young constituted 27.5%, which rose to 34% in 1957 and to 49.5% in 1958. It was considered that the killing was exceptionally high in the 1950s and the state of the herd at the beginning of the 1960s caused anxiety (Rasmussen, 1960), necessitating a ban on hunting in Denmark Strait. In turn, during the years of World Wars I and II the forced cessation of hunting using ships promoted the restoration of reserves. The reduction at present is, however, quite perceptible. Hunting is the main factor responsible for the population dynamics of the hooded seal.

Field characteristics. The under-yearlings are easily distinguished by the two-toned coloration of the skin, i.e., bluish-gray on top and white below. The adult animals are recognized by their large size and contrasting spottiness. The hooded seal can readily be distinguished from the harp seal with transitional (gray spotted) coloration by the former's fairly large blackish-brown and dark brown spots often fusing into fanciful patterns on a gray background with densely scattered spots and dabs in the anterior portion of the body. A positive feature of recognition is the saclike process on the head of adult males, which is quite often inflated through the nostrils (Fig. 212, A, B). Distribution in separate "families" on ice floes during the nursery period is also a useful species characteristic. (K.Ch.)

Economic Importance

The economic importance of the hooded seal in the world hunting industry is quite high. As an object of hunting using ships in the North Atlantic, it occupies second place after the harp seal. The main region of hunting now falls in the international waters near Jan Mayen. Sections



409

Fig. 212. Head of an adult male hooded seal. A—with a "cap" slightly inflated by the nasal cavity (after Mohr, 1963); B—schematic depiction of fully inflated nasal cavity ("cap") (figure by K.K. Chapskii).

of the "polar front" to the north of Newfoundland are of much less importance. In both these regions the hooded seal is caught together with the harp seal. Until recently, hunting was practiced in Denmark Strait and half a million hooded seals were caught there in the 1860s. In good hunting seasons at the end of the last and early in this century, 15 to 20 hunting ships caught 40,000 to 57,000 seals. In the region of Jan Mayen, however, even in the first two decades of this century relatively few hooded seals were caught. Large congregations were not found in this area. The catch rose markedly from the 1920s. In 1926, Norwegians caught 53,000 hooded seals in the expanse from Spitsbergen to Denmark Strait (Sivertsen, 1941).

In the postwar years (from 1956 through 1958), hunting notably decreased in Denmark Strait and was totally banned in 1961. In the region of Jan Mayen, however, it continued at a high level. From 1946 to 1958, it averaged at different times 35,000 - 59,000 - 44,000 seals per annum. The catch of hooded seals in the Newfoundland area (in which Norwegians and Canadians hunt) represented about 10% of the hunt in the Jan Mayen region. In these years the catch averaged 5,700 animals, mainly pups.

409 The Soviets took to hunting the hooded seal in 1955 and continued to do so up to 1967. The ice floes of the Greenland Sea in the region of Jan Mayen constituted the hunting region. Here the harp seal was the main target.

The extent of hunting is depicted in Table 29.

Relative to the harp seal, also hunted in this region, the catch of the hooded seal varied from 10-15% of the total catch in the early years of hunting to almost 70% in some subsequent years.

410 There is nothing specifically different in the hunting of hooded seals using ships compared to harp seals except that the ships have to operate under more severe icy conditions, often approaching each "family" group separately. The hunting operations for some reason or the other involve

409 **Table 29. Catch of hooded seal by Soviet hunting ships in the Greenland Sea (R.Sh. Khuzin)**

Year	Total catch	Pups in total catch
1960	4,575	1,472
1961	11,781	7,101
1962	9,562	3,874
1963	7,303	3,470
1964	8,861	4,706
1965	8,380	5,326

great difficulties as well as much time. Hunting itself is not a very complicated affair due to the slower self-preservation reflexes of the animals in the period of reproduction.

The main problem is locating the rookeries since aerial assistance is not used. Although the hooded seal represents an enticing target (an adult animal yields more fat than a harp seal, while the skin of a juvenile hooded seal is highly valued as a commercial fur), it was not specially sought in the early years of hunting and only whatever came in the way of a ship was taken. Later, however, hunters laid greater emphasis on the hooded seal. After World War II, the Norwegian hunters invariably sought the juveniles so that the catch of pups exceeded that of adults, amounting to 55.5-86% of the total catch. On average, in the first 13 postwar years the Norwegian hunters killed 70% of the juvenile hooded seals available in the Jan Mayen region. The fashion for seal skin overcoats played no mean role in this regard. The hair coat of the pups is distinguished by denseness, moderate luxuriance, excellent color and luster, while the skin is quite durable.

The skin with the subcutaneous fat layer when removed by the hunters (without the flippers) weighs 5 to 11.5 kg (average 9.1) in the case of a newborn but averages 20 kg at the end of lactation. The weight of an adult skin with the fat in early spring (during the breeding season) in the case of males (length along the dorsal surface, *Lc*, 225-260 cm) varies from 45 to 60 kg. The weight of the blubber in males constitutes roughly 60% of the total weight and in females impoverished during lactation 30-40% (L. Popov, 1961). The meat is used as feed in fur animal farms.

To implement rational exploitation of the resources of the Jan Mayen hunting region and to ensure conservation at a stable level for a long time, agreements are imperative between the countries involved in hunting the hooded seal.

Efforts in the field of research should be directed primarily toward an accurate census of the pups of the hooded seal; a comprehensive study of its ecology, including intensity of reproduction; migration characteristics; degree of isolation of the Jan Mayen herd from the western Atlantic (Canadian) populations; etc. The major task is to establish rational norms of permissible kill to prevent the exhaustion of hooded seal resources.

Some measures restricting hunting have already been implemented in Norway and the USSR. These measures provide: (1) restricted hunting in the breeding season in the Jan Mayen region (commencement of hunting not earlier than March 20 and its cessation not later than

May 5); (2) banning the reentry of a ship for hunting in the same season; (3) banning hunting in Denmark Strait; and (4) banning hunting in summer on drifting ice floes north of Jan Mayen Island. (K.Ch.)

ORDER OF WHALES

Order CETACEA Brisson, 1762

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ORDER OF WHALES

Order CETACEA Brisson, 1762

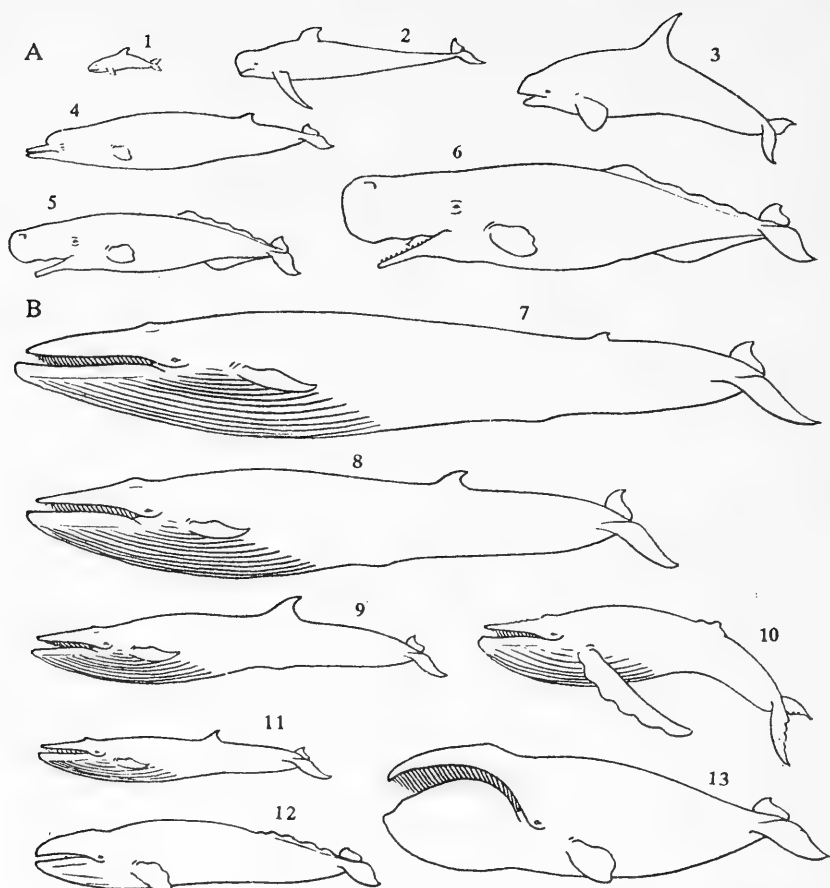
These are highly specialized mammals, totally adapted to aquatic life.

Dimensions vary from moderate to large and these animals are the largest among mammals. Body length and weight range from 1.1 m and 30 to 300 kg in some large dolphins to 33 m and 100 to 120 tons in blue whales (Fig. 213).

The body is streamlined, spindle-shaped or teardrop-shaped, elongated or somewhat shortened: Such a shape offers the least resistance to swimming in water (Fig. 214). In common dolphins the body is better streamlined than in such fast-swimming fish as gray mullets and bonitos (Shuleikin, Luk'yanova, and Stas', 1937). Resistance to swimming in water is also reduced by the reduction of ear pinnae and the placement of mammary glands and teats in special pouches in females and the penis in a special slit in males.

The forelimbs are modified in the form of fin-shaped flippers, which essentially serve as rudders. The hind limbs are totally reduced. At the end of the laterally flattened caudal crest there are paired horizontal caudal flukes without a skeleton. The caudal section of the trunk serves as the main locomotory organ. In most species an unpaired dorsal fin without a skeleton performs the role of a stabilizer while swimming. The head is often massive, sometimes about one-fifth of the body length, and is usually fairly elongated. It terminates obtusely or acutely, or has an extended rostrum, i.e., the so-called "beak". The head in almost all these animals merges without a visible neck into the trunk, which gradually narrows with no sharp boundaries into the caudal crest.

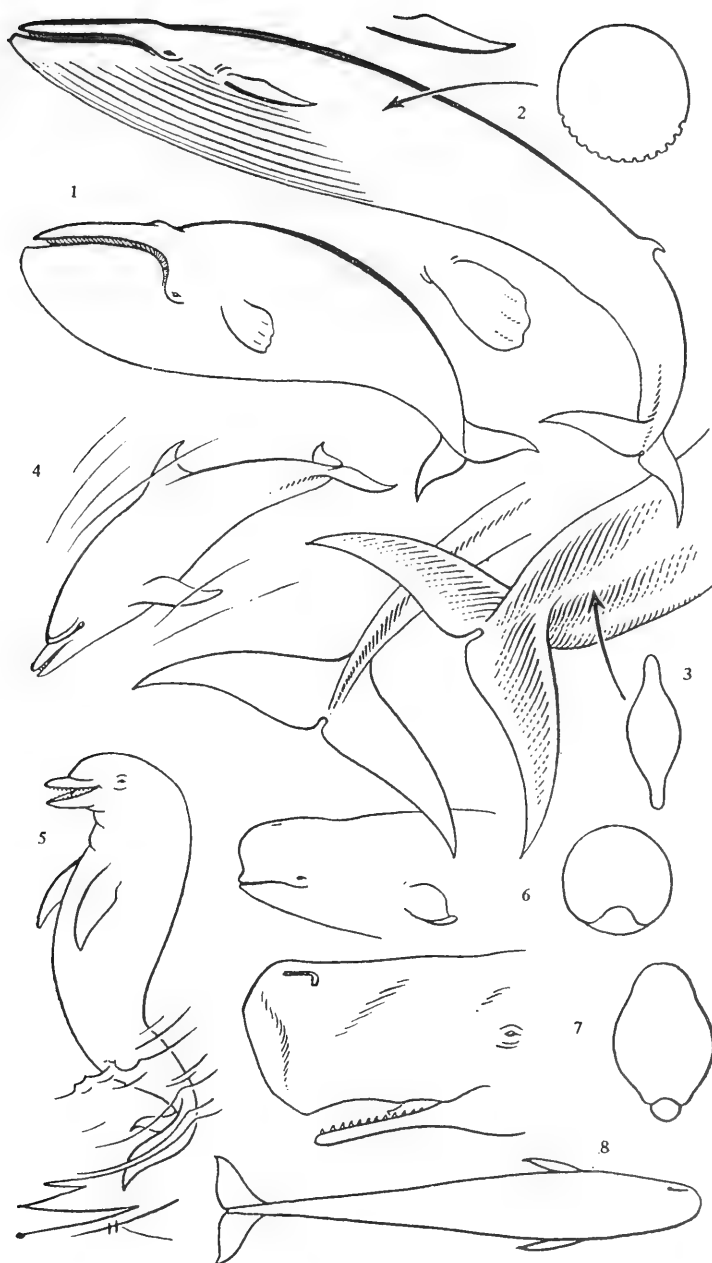
Whales do not have a compact hair coat. Baleen whales have some stray bristles on the snout, typically structured like the whiskers of land mammals. These hairs evidently play a specific role in searching for



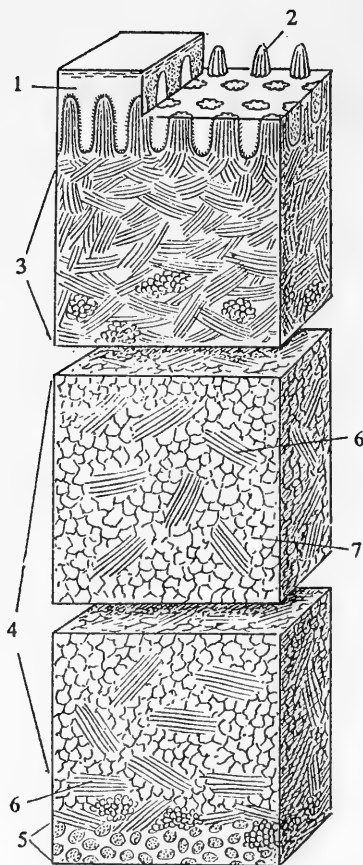
414 Fig. 213. Comparative size of whales (figure by N.N. Kondakov). A—toothed whales: 1—common dolphin, 2—pilot whale, 3—killer whale, 4—Baird's beaked whale, 5—female sperm whale, 6—male sperm whale; B—baleen whales: 7—blue whale, 8—fin whale, 9—sei whale, 10—humpback whale, 11—Minke whale, 12—gray whale, 13—bowhead whale.

massive plankton collections (up to 400 nerve tips present in the follicle of one such hair). In the adult state, among the toothed whales, only the river dolphins possess whiskers: the Ganges River dolphin—*Platanista gangetica* and the Amazon dolphin—*Inia geoffrensis* living in muddy river water. In most of the other toothed whales (except for the white whale and narwhal), whiskers are present only in the embryo.

414 Cutaneous glands are lacking. The skin consists of an epidermis, dermis, and a very thick layer of subcutaneous fatty cellular tissue [blubber] with no distinct demarcation between the last two layers (Fig. 215). The



415 Fig. 214. Characteristic body form of whales (figure by N.N. Kondakov). 1—right whale; 2 and 3—rorquals; 4 and 5—dolphins; 6—white whale; 7 and 8—sperm whales.



416 Fig. 215. Structure of the skin of whales according to V.E. Sokolov.
1—epidermis; 2—dermal papillae; 3—dermis; 4—subcutaneous fatty cellular
tissue; 5—subcutaneous musculature; 6—bundles of collagen fibers; 7—fat cells.

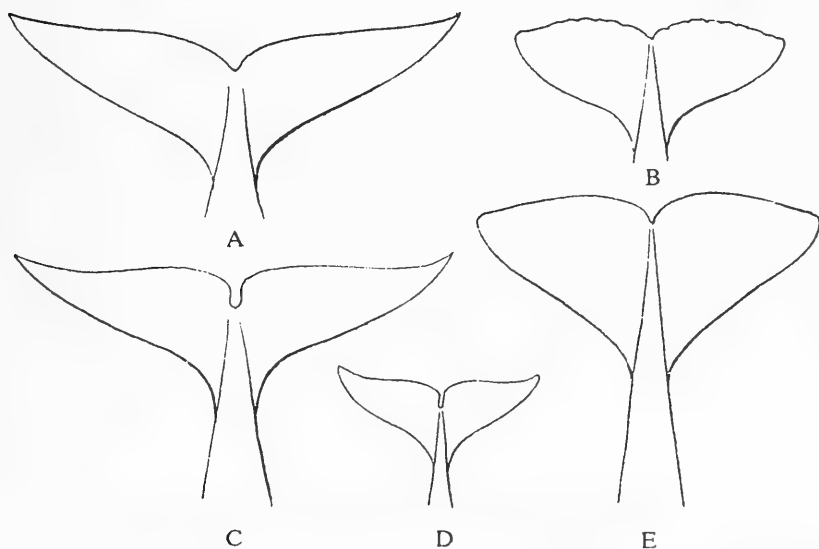
epidermis in the body sections exposed to the maximum resistance of water while swimming (anterior margins of the fins and anterior part of the head) attains maximum thickness. The inner surface of the epidermis has numerous cells in which dermal outgrowths (papillae) grow vertically upward toward the kin surface. The pigmentation of the epidermis determines the body color of whales. At the boundary of the epidermis and dermis, pigment cells—melanophores¹—are visible. The color of some

¹ Numerous white or weakly pigmented spots (scars) of varying size are usually found on the skin of whales. These are scars from bites during fights, attacks by sea lamprey, parasitization by some Protozoa, crustaceans, etc.

416 cetaceans has been correlated with age-related variations (for example, among white whales and narwhals). The dermis consists of a thin layer of dense intertwined bundles of collagenous fibers and papillae rising from this layer into the epidermal cells. In the subcutaneous fatty cellular tissue, straight fascicles of collagenous fibers are considerably larger than in the dermis and widely separated from each other, and the entire space between them is filled with accumulations of fat cells. The thickness of the subcutaneous cellular tissue varies in different seasons: for example, among female fin whales, it is 7.8 cm in December and grows to 12.7 cm by March (Slijper, 1936).

The peculiar structure of the skin of whales evidently promotes development of a laminar flow of water around the swimming animal, with a minimum expenditure of energy when developing high speed.

The caudal flukes (Fig. 216) under the skin cover consist of three layers: one deep and two superficial. The superficial layers are formed of the tendons of *m. longissimus* and *m. hypaxialis lateralis*² (Narkhov, 1937) and spread fanlike into the flukes (Felts, 1966). The deep layer consists



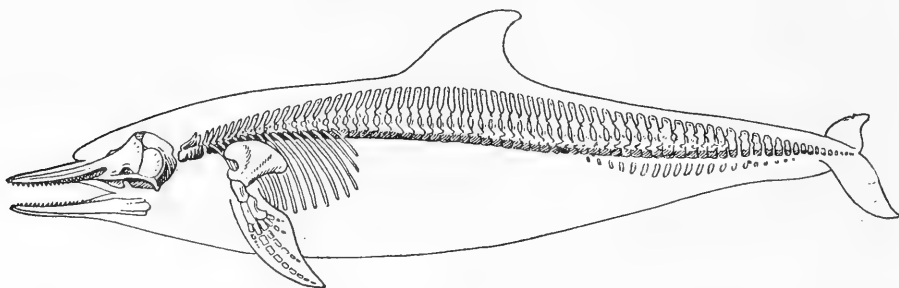
417 Fig. 216. Figure showing structure of the caudal flukes in various species of whales (figure by N.N. Kondakov). A—Atlantic right whale; B—gray whale; C—fin whale; D—common dolphin; E—sperm whale.

² According to A.V. Yablokov (1959), the tendons of these muscles do not reach the caudal flukes.

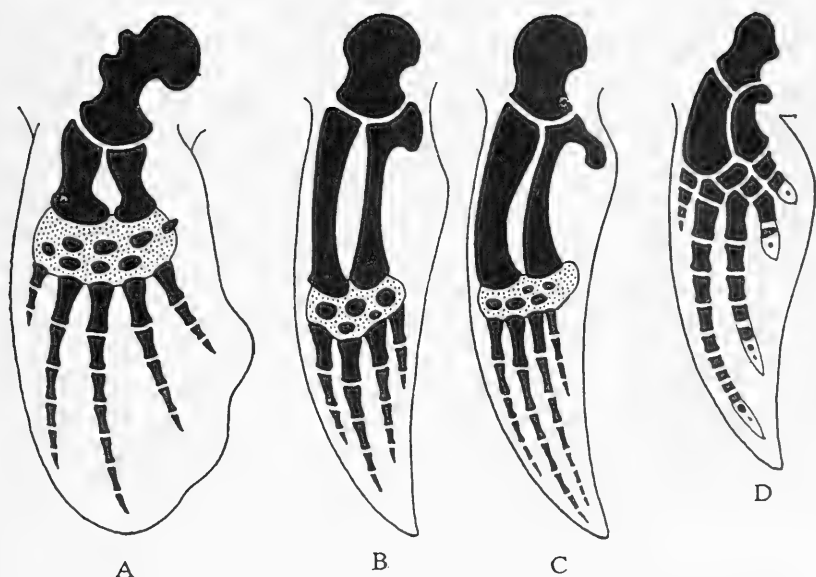
of a fairly dense bunch of large bundles of collagen fibers between which groups of fat cells occur. The caudal flukes are capable of minor independent movements (Zenkovich, 1952). The internal structure of the dorsal fin is similar to that of the deep layer of the caudal flukes. In the fins, along with normal arteries and veins, complex vessels exclusively typical of whales are seen. Each of these vessels consists of a large artery with a very thick middle layer (tunica media) surrounded by 10 to 13 very fine thin-walled veins. The base of the dorsal fin has more than 20 such vessels, which are fewer in number in the caudal flukes and flippers (Tomilin, 1957). These typical vessels are seen in the body parts but differ in structure; their formation is evidently determined by functional requirements.

The elasticity of the caudal flukes can evidently vary during the movement of the animal due to blood pressure controlled by complex vessels and the general distribution system present in the principal supply vessel (Pershin *et al.*, 1970). It is possible that the effect of hydroelasticity in the caudal flukes has a bearing on the swimming of whales.

Skeletal bones essentially have a typical spongy structure and contain a large amount of fat. Clavicles are lacking (Fig. 217). The sternum is highly variable in size, shape, and articulation, depending on the number of ribs attached. The scapula is broad, flabellate [fan-shaped], and has a poorly developed crest. The humerus is extremely reduced. The radius and ulna are also highly reduced, flattened, and greatly broadened
 417 (Fig. 218). Flattening of the limb bones is evidently associated with the limb performing a typically new function similar to that of the aileron of an airplane wing. In view of the fact that the load on the limb is perpendicular to it, the limb is flattened in the same direction (Druzhinin, 1924; Yablokov, 1959). All the bones of the free limb are firmly interconnected and sometimes even fused, and with a common integument. Only the shoulder joint is movably articulate. Nevertheless, antebrachial muscles are preserved in the majority of whales. More often than among



418 Fig. 217. Skeleton and body contour of the common dolphin, *Delphinus delphis* (figure by N.N. Kondakov).

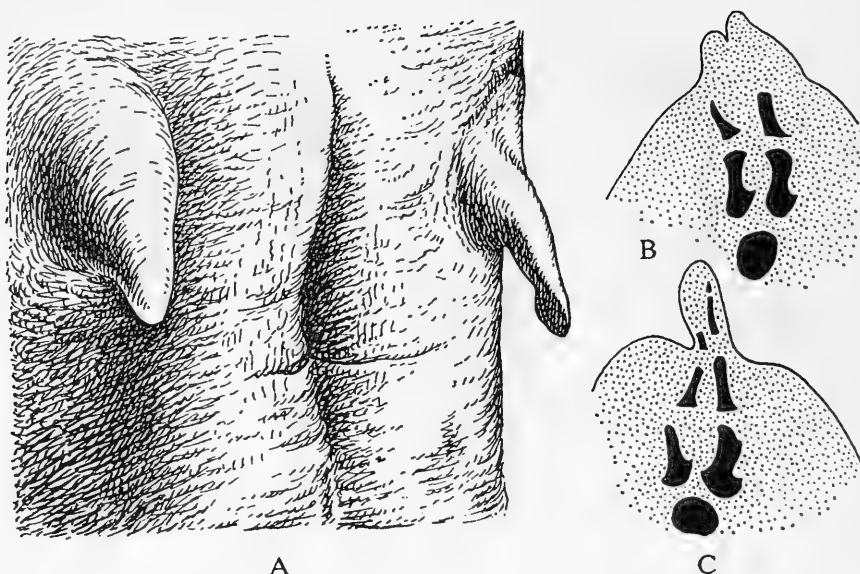


418 Fig. 218. Skeleton of the limbs of whales (schematic). A—bowhead whale; B—fin whale; C—blue whale; D—common dolphin (figure by N.N. Kondakov).

other mammals, the fusion of the carpals is noticed. The number of digits is four or five. The number of phalanges in the middle digits is more and in the outer ones less. The number of phalanges in the embryo is more compared to the adult, i.e., they reduce in number during the course of ontogenesis (Kükenthal, 1889; Yablokov, 1959).

The hind limbs form in a fairly early embryonic stage but soon disappear. Their rudiments are very rarely preserved. Among adult whales, only the rudiments of the pelvis arranged in the musculature, in the form of two bony shafts (fused ilium, ischium, and pubis), are preserved of the hind limbs. Their articulation with the vertebral column has disappeared but the muscles of the urogenital system are attached to them and, obviously for this reason, their total reduction has not taken place (Yablokov, 1959).

The vertebral column consists of only four sections: cervical, thoracic, lumbar, and caudal. Sacral vertebrae are lacking due to the disappearance of the hind limbs. The cervical section is represented by seven highly reduced vertebrae which may be fused into a single unit or several groups. In the rest of the sections, the number of vertebrae varies. Transverse and spinous processes attain large proportions. Hemal arches, similar to those in the lower vertebrates, appear in the caudal section.



419 Fig. 219. Rudiments of the hind limbs of the sperm whale. A—outer view; B
and C—X-ray pictures (figure by N.N. Kondakov, after A.A. Berzin, 1970).

The number of ribs varies from 10 to 17 pairs. The anterior two to
eight pairs are normally joined to the vertebrae; the posterior ribs have
418 neither capitulum nor collum and are articulated only to transverse verte-
bral processes. The anterior eight pairs of ribs are joined to the sternum.
The thoracic cage, unlike in most land mammals, is not laterally com-
pressed but round in cross section or slightly flattened dorsoventrally.

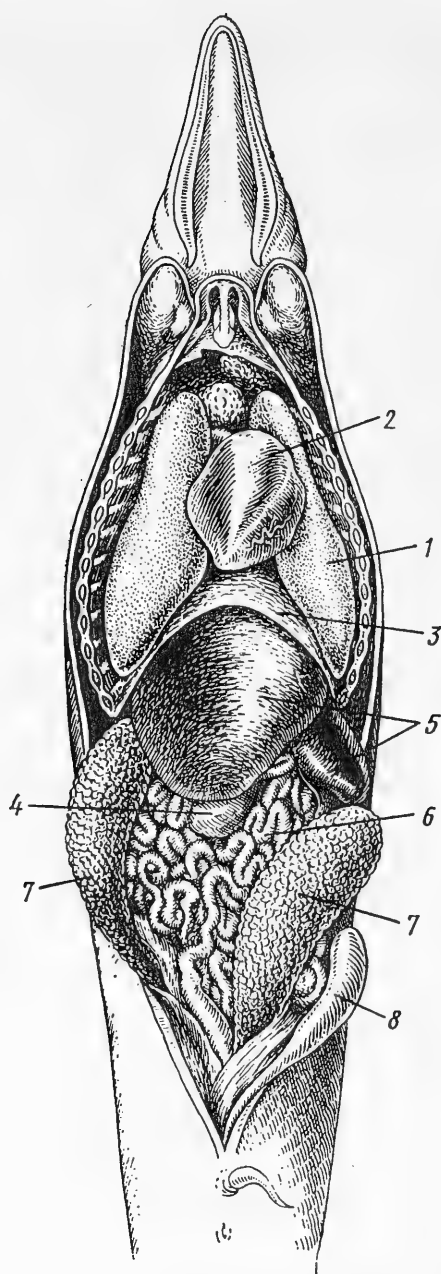
The bones in the skull of whales are arranged symmetrically or asym-
metrically. In the latter case, the bones on the right side are broad-
ened and shifted leftward while the left ones are thickened. Some bones
may overlap others. The cranial section is shortened and rounded. The
supraoccipital bone is highly developed and joined with the frontal bone
anteriorly while the parietal bones are shifted laterally. The nasal bones
are small and the outer bony apertures are shifted far backward and lie
directly anterior to the neurocranium. The nasal passages are short and
run fairly vertically. Maxillary and premaxillary bones and the vomer are
highly extended and form a rostrum. The bony palate is elongated due
to the large pterygoid bones, as a result of which the choanae appear
419 displaced backward. The mandibles are long and have a rudimentary
coronoid process, which is sometimes lacking.

In the adult state, only the members of the suborder of toothed
whales possess teeth, which are homodont and serve only to hold and kill
the prey. In the embryo of baleen whales, teeth begin to form but soon

cease to grow and are resorbed. Among adult baleen whales, the teeth are functionally replaced by special, characteristic horny formations of the palatal epithelium, the so-called "whalebone" [baleen] which serves to strain the tiny planktonic organisms on which these whales feed. The triangular plates of the whalebone are fixed along the edge of the upper jaw parallel to each other in such a way that the smaller side of the triangle falls toward the upper jaw while the larger side is turned outward and the hypotenuse is inside the oral cavity. The inner part of the plate of the whalebone is split into innumerable fine and long keratinous filaments. The baleen plates are slightly separated from each other and the filaments of the neighboring plates are intermeshed to form a gauze-like structure. When the whale swims with its mouth open, water passes through this structure continuously while the planktonic organisms are retained on its surface. By closing its mouth, the whale pushes out the water from the oral cavity with its tongue, which also helps to push the food particles into the esophagus: whales do not masticate food. The tongue is well developed and soft lips are absent. Salivary glands are either altogether lacking or are rudimentary.

The stomach is complex and consists of three to fourteen sections (Fig. 220). This complexity is explained by the absence of food mastication. The length of the intestine varies: it may be five or six times the body length as, for example, among baleen whales (Mysticeti) or among species of the family of beaked whales (Ziphiidae); 15 to 16 times among sperm whales and bottlenose dolphins; and up to 32 times among La Plata dolphins (*Pontoporia blainvillei*). The liver is relatively small and a gall bladder is absent. The pancreas is elongated and faintly lobular, far more rarely disjunct; its ducts open into the bile duct.

420 External nares (blowhole) are paired among baleen whales and unpaired among toothed whales, shifted to the top of the head, and have valves that close them during diving. Among the toothed whales, the nasal passage above the skull has special air sacs. Elongated laryngeal cartilages of toothed whales enter the choanae and thus maintain a constant contact between the larynx and the air sacs located above without interruption even during swallowing. The trachea and bronchi are shortened. The short passages transporting air accelerate respiration. The lungs are single-lobed with highly developed smooth muscles. The bronchioles have a series of smooth muscle sphincters (among toothed whales) or contain a large number of muscle fibers in the upper portion of the alveolar septa (among baleen whales). The connective tissue of the lungs is highly elastic. Lymphoid tissue is almost totally absent. The number of alveoli is relatively large and their dimensions somewhat larger than among land mammals. The epithelium of the bronchi and



glands is almost devoid of mucous cells, which is evidently associated with the absence of dust in the air intake (Slijper, 1958a). Alveolar septa contain two layers of capillaries and a very large amount of elastic fibers. All the bronchi have a ciliate epithelium and are surrounded externally by cartilage of irregular shape. These cartilages are also seen in the terminal bronchioles (not found among beaked whales, *Berardius*).

Whales can survive without breathing for quite sometime and remain under water from 2-10 to 30-40 min (up to two hours, according to some authors). They are insensitive to large amounts of carbon dioxide in the blood; its accumulation does not regulate their respiration, as in land mammals, but an oxygen deficit in the blood does.

The long duration of diving is ensured by the large capacity of the lungs, insensitivity of the respiratory center of the brain to the accumulation of carbon dioxide in the body, high content of myoglobin, and slightly higher oxygen-holding capacity of the blood due to its higher hemoglobin content and its high concentration of erythrocytes (Irving, 1938; Taarra, 1950; Korzhuev and Bulatova, 1952; Kleinenberg, 1956a, 1957).

421

Hemoglobin content in 100 ml of blood, g

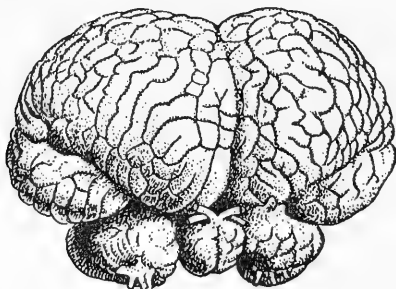
Sei whale	15.6
Sperm whale	15.8
Cow	12.4
Man	13.0

Respiration in whales can usually be divided into several stages: (1) exhalation after prolonged diving; (2) intermediate brief inhalation and exhalation; and (3) deep inhalation before prolonged diving. During intermediate inhalation and exhalation, the whale does not dive very deep, surfaces almost always vertically, and breathes at regular intervals. The number of intermediate inhalations/exhalations varies among different species; the longer the animal remains under water during diving, the greater the number. There is a particular reflex movement during inhalation: the animal strikes the water with its caudal fin in an up and down movement which invariably keeps the top of the head with the blowhole afloat (Tomilin, 1957). Exhalation can commence even under water, as a result of which the air expired under pressure forms a water jet that is generally characteristic in shape and size for various species.³

³ Apparently, the jet or fountain may also be formed as a result of the condensed vapor present in the warm air expired (in high latitudes) and also as a result of holding and spraying of the water which remains, as the whale surfaces, in the cavity in which the blowhole is located.

Some whales are capable of diving to great depths (for example, sperm whales can sink deeper than 1,000 meters). The quick surfacing of the animal from a great depth should liberate the gaseous nitrogen dissolved in the blood under the high pressure generated during diving. Otherwise the blood vessels would become clogged with nitrogen bubbles, leading to caisson disease and even to the death of the animal. But whales do not suffer from this disease. This is probably explained by the fact that the amount of nitrogen present in the lungs slightly exceeds the nitrogen-holding capacity of the tissues while no more air enters the lungs during diving (unlike what happens in divers).

The brain in most respects is highly differentiated but in many other respects has preserved extremely primitive features that are not found among the members of other orders of mammals (Fig. 221). These differences are mainly: significantly narrow cortex in cross section while layers I and V-VI, the oldest in evolution, are predominantly developed; overall high cellular content of the cortical plate; and developmental features and ratios of the zones of old and intermediate cortex (Filimonov, 1949). The weight of the brain in absolute terms is maximum in mammals but is insignificant in relation to the body weight (especially among large whales). The brain of white whales weighs 2,180 to 2,340 g (Kleinenberg *et al.*, 1964), fin whales 6.5 to 7.2 kg, and sperm whales 7 to 8 kg (Kojima, 1951; Janes, 1952). Large convolutions and longitudinal fissures are seen in the short rounded form of the brain. Intense development of the cortex of the hemispheres of the forebrain is a characteristic feature. Without exception, the cortex houses the paleocortical, archicortical, and interstitial zones (Filimonov, 1949). The cerebellum attains large dimensions (up to one-fifth of the weight of the entire brain). The hypophysis is highly developed.



422 Fig. 221. Brain of the common dolphin, *Delphinus delphis* (figure by N.N. Kondakov).

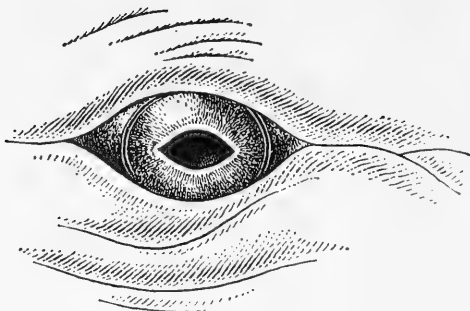
The structural peculiarities of the cetacean brain are associated with the high degree of development of the higher nervous activity of these animals. Many species of whales are easily tamed and trained. With respect to higher nervous activity, some whales (for example, the bottlenose dolphin) may be placed among the higher mammals although lower than the anthropoid apes (Voronin, 1970).

422 Reduction of the rhinencephalon is a characteristic feature. The bulbus olfactorius is lacking in most whales (Kükenthal and Ziehen, 1893)⁴ and the lobus hippocampi are poorly developed. The V and VIII pairs of cranial nerves associated with the sensitivity of the facial region and auditory organs are highly developed. Among bottlenose dolphins (*Tursiops truncatus*), the following features of the brain have been noted (Kruger, 1959): a prominent flexure between the mesencephalon and the diencephalon; reduction of tactile thalamic region, evidently associated with the absence of hairs in adult animals (this is true of most toothed whales); intense development of n. ventralis medialis, definitely suggesting that whales have a sense of taste (although many investigators refute this); and so forth. Among some toothed whales (narwhal, pilot whales, white whales, and common propoises), a small number of typical pits with minute processes at the bottom have been noticed on the surface of the root of the tongue. They evidently function as organs of chemical perception (Yablokov, 1957, 1961a); taste buds are found in them (Yablokov *et al.*, 1972) as well as many efferent ducts of the albumen and mucous glands.

The eyes are small (Fig. 222). The cornea and sclera attain considerable thickness and the optic muscles are well developed. The crystalline lens has a characteristic spherical form. Eyelids are not developed. Vision is evidently monocular and myopia is typical (Kellogg, 1928; and others). The lachrymal glands are reduced and the nasolachrymal passage is lacking. An oily secretion from Harder's gland protects the eye from the mechanical and chemical action of water. Conjunctival glands, not found among other mammals, are present (Weber, 1886). The olfactory organs and Jacobson's organ are reduced.

Sense organs among baleen whales and some toothed whales (for example, the Amazon dolphins, *Inia*) are represented by vibrissae disposed on the snout and sometimes all over the trunk (Fig. 223). Numerous nerve ends approach the roots of the vibrissae surrounded by blood lacunae (Japha, 1910). Among all whales, the sensory nerve endings rise

⁴ The bulbus olfactorius has been described (Flatau and Jacobson, 1899; Filimonov, 1949) in the bottlenose whale, *Hyperoodon rostratus*, the blue whale, *Balaenoptera musculus*, and the fin whale, *B. physalus*.



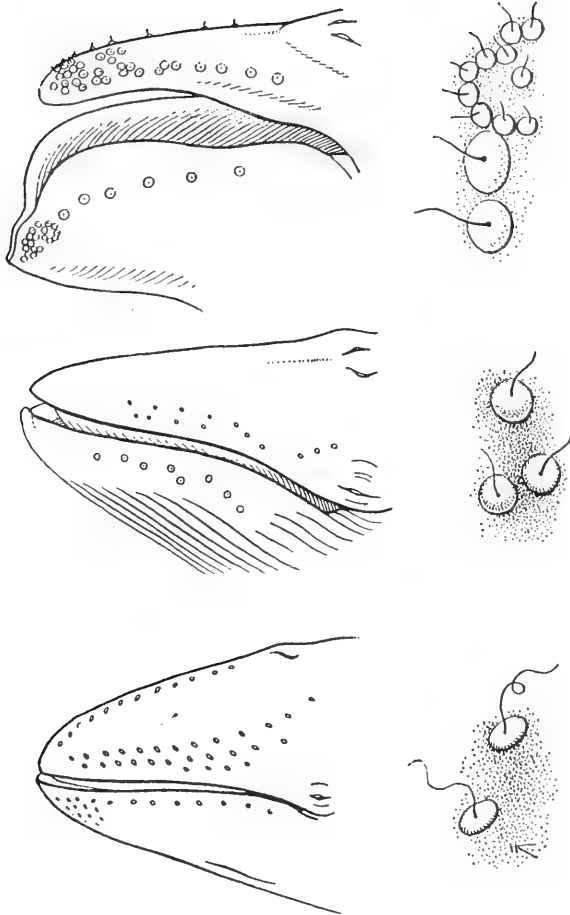
422 Fig. 222. Eye of the fin whale, *Balaenoptera physalus* (figure by N.N. Kondakov).

along the dermal papillae almost directly at the outer surface of the skin so that the entire surface of the body appears well innervated.

423 The auditory organs are highly modified (Fig. 224). The concha is reduced. The external auditory meatus opens outward behind the eye as a tiny aperture; its lumen is invariably covered. It is possible that the rudimentary auditory meatus may serve as an independent organ perceiving pressure changes (Yamada, 1953). The tympanic membrane bends outward (among baleen whales) or inward (among toothed whales), and is externally covered among baleen whales by a typical ear plug of keratinous epithelium and cerumen.⁵ In view of the fact that the petrous tympanicum is not only isolated from the other skull bones, but also surrounded by special air cavities, it is possible that whales perceive sound signals through the auditory meatus. It has been suggested that sound is perceived through the body surface (especially the head), transmitted to the auditory zone, and that the petrous tympanicum, which is capable of vibrations, acts as a resonator. It has also been suggested that the lower jaw is also capable of perceiving sound from the external environment and transmitting it to the auditory organs.

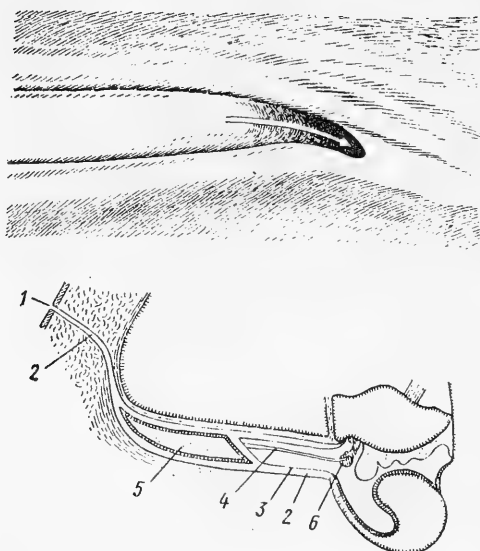
Whales are capable of receiving a wide range of sound waves: from 150 to 120 - 140 thousand Hertz (Kellog, 1953; Slijper, 1955, 1960; Bullock *et al.*, 1968), i.e., even ultrasonic vibrations. The high degree of development of the auditory section of the brain of toothed whales points to their particularly acute sense of hearing, which is almost unique among mammals. Among baleen whales, hearing is inferior to that among toothed whales but better than that among land mammals (Ogawa and

⁵ The age of whales can be determined by counting the layers in a slice of this plug (Purves, 1955).



423 Fig. 223. Vibrissae of whales. Top to bottom: Atlantic right whale, fin whale, and gray whale (figure by N.N. Kondakov).

Arifuku, 1948). Whales, like bats, are capable of echolocation (Kellogg, 1958). Since vocal cords are lacking, whales cannot produce sound by the methods ordinarily used among mammals. However, that they do produce diverse sounds has long been known. Evidently they result from vibrations of the lower portion of the nasal septum (Tomilin, 1957) or vibrations of the folds of the outer valve due to passage of air from the dorsal nasal sacs (Yablokov, 1961b). It should be noted that dolphins have at least two systems of sound production: they are capable of simultaneous production of location signals and whistles. It has been
424 suggested that whistles are produced by means of the larynx; impulse



424

Fig. 224. Structure of the auditory organs in the fin whale, *Balaenoptera physalus*. Top—outer view; bottom—section (figure by N.N. Kondakov). 1—outer opening; 2—membrane; 3—tympanic membrane; 4—ligament between tympanic membrane and malleus; 5—ear plug; 6—auditory ossicles.

signals are apparently produced by the air sacs (Evans and Prescott, 1962; Norris, 1964). The typical structure of the frontal section of the skull and the disposition of the fatty “lens” anterior to it enable the animal to judge the direction of sound waves (Romanenko *et al.*, 1965).

The blood circulatory system of whales has several characteristic features, some of which are also encountered in other aquatic and terrestrial mammals (Slijper, 1959): (1) arterial rete mirabile is present on the inner side of the vertebral column and particularly well developed in the regions of the neck, thorax, between the ribs, at the base of the brain, and around the spinal cord. It is formed of a large number of sinuous arteries of the muscular type interconnected by several anastomoses. The histological structure of the vessels points to their capacity to modify considerably the volume of blood flowing in them; (2) the venous rete mirabile is present at the base of the skull and is particularly massive in the abdominal zone; (3) an expansion occurs in the hepatic vein (lacking in baleen whales); (4) two vertebral veins running along the ventral side of the vertebral column are almost identical in diameter throughout their length and lack valves, indicating that blood can flow in them in both directions: through the major vv. costocervicales they run into the

anterior vena cava and through the veins between the ribs into the posterior vena cava. Since all these features of the blood circulatory system attain maximum development among smaller whales, they are evidently associated not with deep and prolonged diving of the animals, but with frequency of diving and respiration. A reference has already been made to the venous vessels of fins typical of whales (arteries surrounded by small veins). In addition to the very high (compared to terrestrial mammals) oxygen capacity of the blood, the considerable concentration of sugar and sodium chloride in it is a characteristic feature of whales. This is evidently associated with the deposition of additional reserves of food required by the animal during prolonged underwater residence. The diameter of erythrocytes in whales varies from 6.6 to 10.0 microns (Lenfant, 1969).

The body temperature of whales is similar to that of land mammals and varies from 35 to 40°C (the upper limit was recorded among wounded whales or dolphins caught after chasing). The maintenance of a high body temperature in water, which conducts heat many times better than air, is facilitated by the thick layer of subcutaneous adipose tissue. Killed whales 60 h after the moment of death and in cold water recorded a temperature close to 30°C⁶, i.e., only 6-7°C loss of heat during this
 425 time (Zenkovich, 1938). The temperature of the outer layers of the skin among whales is close to the temperature of the surrounding water. This is achieved by minimal heat dissipation by the body as required for normal activity in such a highly heat-conducting medium as water. In the case of over-heating of the whale body (for example, on rapid and prolonged swimming), dissipation of heat occurs from the entire body surface but more intensely from the surface of the fins.

Compared to land mammals, the musculature of the trunk and limbs has undergone the most intense modification. As a result of losing the locomotory function, the following muscles in the forelimbs are very weak: m. romboideus, m. serratus, m. levator scapulae, and m. infraspinus; m. trapezius and m. teres minor are totally reduced; and m. deltoideus, m. subscapularis, and m. panculus carnosus are highly developed. In the trunk, m. latissimus dorsi and m. ileo-costalis passing through the dorsal side of the vertebral column as also m. hypaxialis lateralis and m. hypaxialis medialis passing along its ventral side are particularly well developed. The former are attached anteriorly to the skull and the latter to the lateral processes of the posterior thoracic

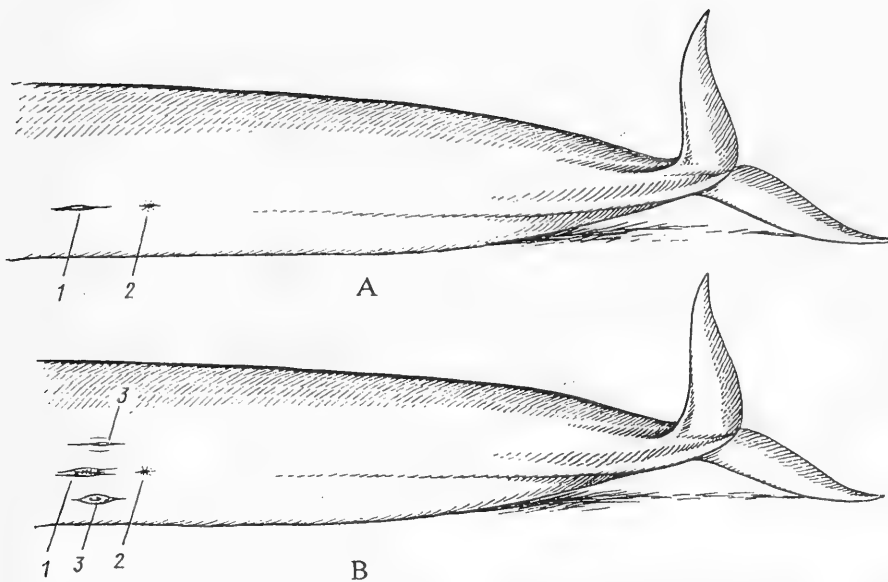
⁶ The high body temperature of the killed whales may also have been partly maintained by the process of putrefaction; nevertheless, this fact points to the considerable heat-insulating capacity of the subcutaneous adipose tissue.

vertebrae and to the last of the ribs; posteriorly, these muscles are attached to the caudal vertebrae and (Narkhov, 1937) partly transit into massive tendons running into the flukes and diverging fanlike there.

The kidney of whales is multilobulate and relatively much larger than in land mammals (Slijper, 1958a). The urinary bladder is small; the absence of a sphincter in its neck facilitates frequent urination in small quantities which possibly may serve as a signal for other whales (Yablokov, 1961a). Whales evidently do not swallow sea water and the required moisture is provided by the food intake in addition to the water of metabolism. The absorption capacity of the kidneys of whales is not so high as to extract fresh water from the swallowed sea water. The concentration of sea water was found to be more than that of the urine (if whales swallowed sea water, this ratio would be reversed) (Table 30).

The testes are located in the abdominal cavity. In blue whales, the length of the testes may reach 45 cm and the weight 45 kg (Slijper, 1966). Of the other glands, only the prostate is present. The penis is long and narrows gradually toward the tip; at rest, it lies in a special sheath. At its base, the penis bends in an S-shape. An os penis is lacking except in the right whale, *Balaena glacialis*. The cavernous tissue is poorly developed in the penis. The crus of the crura penis are attached to the rudimentary pelvic girdle; here, mm. bulbo- and ischiocavernosi are separated. Among adult females, the ovaries are partly or wholly surrounded by an extensive infundibulum of the oviduct. The oviducts extend into the bicornuate uterus, which has longitudinal folds on the inner surface. The portio vaginalis enters the vagina. The outer slitlike genital opening is surrounded by small liplike bulges between which the boneless clitoris is located. Ureters open into the vulvar region; there is no sinus urogenitalis. The vagina contains several ringlike folds which probably perform the role of valves, protecting the genital system from water entering into it during copulation and whelping. In female baleen whales, the genital opening and the anus are separated from each other by a considerable distance while in toothed whales, these are located in a common sac and are surrounded by a common sphincter (Fig. 225). The males are capable of fertilizing throughout or for much of the year.

Ovulation among whales is perhaps stimulated by copulation (Sokolov, 1950, 1954; Sleptsov, 1952; Tomilin, 1957; Yablokov, 1959) but the recovery of spermatozoa in the vagina of female common dolphins
427 having mature but not opened-up follicles in the ovaries casts doubts on this assumption (Sokolov, 1961). On fertilization, the corpus luteum of pregnancy develops in the ovary and, after resorption, traces of it are preserved for a long time (presumably throughout life) in the form of a corpus albicans. The age of the female can possibly be determined by



427 Fig. 225. Zone of disposition of the urogenital organs in the fin whale, *Balaenoptera physalus*. A—male; B—female (figure by N.N. Kondakov). 1—genital opening; 2—anal opening; 3—sac for mammary teats.

counting these bodies. Among pregnant females, two or three fetuses can be found in the uterus at the commencement of pregnancy but shortly thereafter only one is found. The placenta is diffuse, of the epitheliochoreal type (Zhemkova, 1965), and may partly extend into the second horn of the uterus. In the late stages of pregnancy, the embryo is usually situated with the tail toward the womb exit. The lobes of the flukes are convoluted, the dorsal fin (when present) bent down towards the back, and the flippers turned towards the tail. The sex ratio of embryos is roughly 1:1 (Table 31).

Birth takes place under water. The calf is born fully developed and capable of independent movement; its body proportions are highly similar to those of adults (Zemskii, 1958a) but its length up to 1/4 to 1/2 that of the mother. Some female whales can be fertilized soon after parturition, during the lactation period. The calves are suckled under water, the duration of each suckling being short (a few seconds). The calf holds the teat of the mother (Fig. 226) between its tongue and upper palate.

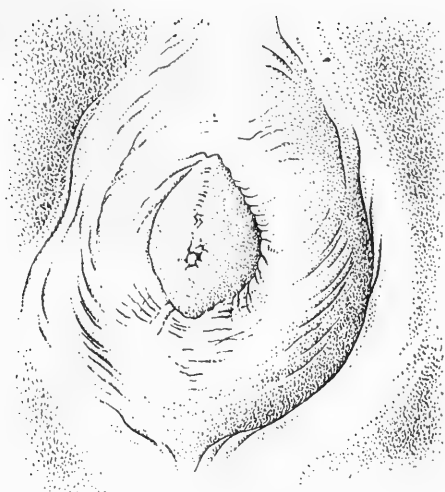
428 An exception is the sperm whale calf, which holds the teat in the corner of its mouth (Slijper, 1966). Milk is sprayed into the oral cavity of the calf by the contraction of special muscles in the female. Newborn calves feed very frequently; for example, calves of bottlenose dolphins suckle

Table 30. Composition of the urine of whales (Fetcher, 1939)

Whale	Number of determinations	°C	Concentration, mm/liter						
			Urea	Na	K	Ca	Mg	Cl	SO ₄ PO ₄
Sei whale	1	2.49	400	330	54	5	—	370	38 21
Sei whale	4	—	420-650	—	—	—	—	260-370	33-43 23-27
Sei whale	4	2.46	380-530	240-290	36-82	0.3-2	1.6-4.1	180-370	36-45 16-41
Fin whale	5	—	250-420	230-330	56-72	1.8-5.3	2.5-5.8	260-370	— 7.1-41
Fin whale	2	—	380-430	270	67	3.3	6.6	250-390	31-40 7.9-41
Blue whale	1	2.50	420	—	—	—	—	340	— 61
Pilot whale	1	2.01	480	—	—	—	—	180	— —
Dolphin	2	2.28-3.41	480-840	—	—	7.0	10	170-240	— —
White whale	1	3.23	570	—	—	18	21	39	5.9 34
Sea water		2.23	—	490	9.8	10	54	540	27 —

Table 31. Sex ratio among whale embryos (Mizue and Jimbo, 1950; Mizue and Murato, 1951)

Particulars	Fin whale		Sei whale		Blue whale		Humpback whale		Sperm whale		Total	
	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
Number of specimens	174	157	81	97	50	62	19	17	247	288	571	621
Percentage ratio	52.5	47.5	45.5	54.5	44.6	55.4	52.8	47.2	46.2	53.8	47.9	52.1



427 Fig. 226. Teat of a lactating female fin whale, *Balaenoptera physalus* (figure by N.N. Kondakov).

roughly once every 26 min day and night (McBride and Kritzler, 1951). The mammary glands of the female lie along the sides of the genital opening. Two teats (one on each side) lie in slitlike folds and project outward only during lactation. Female whales produce a large amount of milk daily: from 200 to 1200 g among dolphins, up to 90 to 150 liters among fin whales, and 200 liters among blue whales (Sleptsov, 1955). The milk is thick and usually cream-colored. Its surface tension is 30 times more than that of water, which is particularly important considering that suckling takes place under water (the milk spray does not spread on water). The nutritive value of whale milk is very high (Tables 32, 33, and 34).

A different composition of the milk of fin whales has been given by Ota *et al.* (1955) (Table 33).

During the period of suckling the growth of calves proceeds very rapidly: for example, by seven months of age the calf of a blue whale had grown to 16 m from 7 m at birth, i.e., the average daily increment of length was 4.5 cm (Slijper, 1960).

Sexual dimorphism among whales is manifest mainly in the differences of body length between males and females. Among baleen whales, the females are larger than males while the converse is true in most toothed whales. Whales are mainly herding animals and live in schools of a few animals to hundreds and thousands. They are encountered

428 **Table 32. Composition of the milk of large whales (g, averages) (Zenkovich, 1952)**

Species	Fat	Dry residue	Water
Fin whale	43.57	13.50	42.93
Blue whale	40.25	13.70	46.05
Humpback whale	39.93	14.02	46.05
Gray whale	53.04	6.38	40.58
Sperm whale	37.30	8.00	54.70
Cow	3.7	21.7	77.3

428 **Table 33**

Fat	Protein	Water	Lactose	Inorganic matter
33.0	13.3	53.4	0.3	1.0
31.8	12.3	55.0	0.2	0.7
32.5	10.5	54.1	1.4	1.4

428 **Table 34. Composition of the milk of small whales (g) (Ural'skaya, 1957)**

Species	Fat	Protein	Sugar	Dry residue	Ash	Water
Common dolphin	43.71	5.62	1.45	7.53	0.45	48.76
Common dolphin	41.56	4.88	1.49	6.82	0.45	51.62
Common porpoise	45.80	11.19	1.33	13.09	0.57	41.11
Common porpoise	33.90	5.22	1.28	7.10	0.60	59.00
Bottlenose dolphin	46.10	11.55	1.57	13.50	0.38	40.50

along coasts as well as in the open sea. Some are capable of ascending along major rivers opening into the sea while some species are regularly confined to rivers. The food of many is specialized; planktophagous, teuthophagous, ichthyophagous, and sarcophagous animals are known (Tomilin, 1957). Whales include fast swimmers (for example, killer whales and many dolphins) and relatively slow-moving animals (gray whales). Most whales regularly remain on the surface while some (for example, sperm whale) can dive to great depths.

The population of the various species of whales is not identical.

Some whales are most numerous and can be found in thousands of schools (common dolphin) while others are very rare and only a few sightings have been reported (some members of the genus *Mesoplodon*

(beaked whales) dwarf sperm whale, and false killer whale). Natural fluctuations in population have not been studied but can hardly be significant. As a result of senseless hunting, the population of many species of whales has sharply decreased. Thus, right whales and gray whales have come close to total extinction. International conventions have imposed a total ban on the hunting of these whales and their population is now slowly recovering. The hunting of even sperm whales and fin whales, numerous in the recent past, has to be totally banned to maintain their population at the present level. A sharp reduction in whale hunting or its total ban for several years, followed by rational and strictly controlled hunting, should be considered.

Periodic migrations are characteristic of many whales. Among some species, the distance covered during migration is relatively small (Azov-Black Sea common porpoise migrates from the Azov Sea into the Black Sea and back) while migrations among others cover long distances: some large whales travel from tropical waters to high latitudes.

Most whales are monogamous. Periods of mating and whelping are usually prolonged. They give birth to one (rarely two) calves. The maternal instinct is strongly developed among females.

Apart from man and the killer whale, there are no enemies of cetaceans.

Cetaceans are universally infected with endo- and ectoparasites (crustaceans). The latter are particularly typical of large whales.

Whales are found in all the oceans, in most of the world seas, and in some rivers and lakes. Two factors determine the distribution of whales: food and water temperature. Some species are widely distributed and are encountered in warm as well as cold seas (some species of the dolphin family), others have a small range (gray whales inhabit the subtropical moderate and cold waters of the North Pacific Ocean and the Chukchi Sea), still others are even more restricted (narwhals do not leave the Arctic waters), and finally, the ranges of river, lake, and estuary forms are altogether insignificant.

At present, relatively few fossil remains of whales are known. Remains of the more primitive of the known whales have been found in the Middle Eocene of North Africa. There is no unanimity of opinion regarding the ancestors of whales. Some scientists support the origin of whales from ungulates, with which they share many common features, such as diffuse placenta, bicornuate uterus, and complex stomach. The number of chromosomes and the reaction of the precipitation of serum proteins of whales confirm this hypothesis (Makino, 1948; Boyden and Gemery, 1950). Based on the structural similarity of the skeleton and the dental system of extinct whales with the primitive carnivores (creodonts),

some scientists assume that the whales originated from the latter. A view has been expressed that the ancestors of whales were much older than creodonts, i.e., cretaceous insectivorous forms (Slijper, 1958a). Some authors (Beddard, 1900; Kükenthal, 1900; Hosokawa, 1950; Kleinenberg, 1958; Yablokov, 1964; Anderson and Jones, 1967) suggest a diphyletic origin of the contemporary order of cetaceans, i.e., that the baleen and toothed whales evolved from different ancestors and that their evolution proceeded by convergence and not divergence; hence it would be more correct to regard these suborders as orders. In confirmation of this hypothesis, numerous morphological differences between the baleen and toothed whales are cited but such evidence cannot be regarded as sufficiently convincing.

The ancient whales, Archaeoceti, are sometimes regarded as convergent with other whales although they have nothing common in phylogeny and hence should not be included in the order of cetaceans (Yablokov, 1964). But even this assumption is not supported by adequately convincing data (Mchedlidze, 1970).

The systematics of Cetacea has not been properly worked out. As mentioned earlier, even the content of this order has been disputed by some. The composition of some families and subfamilies has also not been conclusively established. Usually (Simpson, 1945), three suborders are distinguished in the order Cetacea: modern toothed whales (Odontoceti Flower), baleen whales (Mysticeti Flower), and extinct whales (Archaeoceti Flower). Sixteen families (nine are extinct) and 173 genera (of which 137 are fossil forms) are usually recognized in the order. The total number of contemporary species of the order is 81 (Hershkovitz, 1966). The USSR is host to 6 contemporary families, 19 genera (roughly 52% of the world fauna), and 23 species (roughly 28% of the world fauna) (Tomilin, 1957). The suborder Archaeoceti comprises three families: Protocetidae Stromer (Middle Miocene), Dorodontidae Miller (Eocene and Miocene), and Basilosauridae Cope (Eocene and Oligocene), and 14 genera (Simpson, 1945). The family Protocetidae includes short-bodied forms such as *Protocetus* with a length of not more than 2.5 m and also long-bodied animals (in the available long bodied form of *Eocetus*, the skull alone measures 120 cm in length). Evidently, *Eocetus* was the source of the family Basilosauridae while *Protocetus* and *Pappocetus* gave rise to the members of Dorodontidae (Deshaseux, 1961).

The family Dorodontidae comprises animals 8 to 9 m in length with an elongated and flexible cervical section and serrate cheek teeth while the family Basilosauridae includes animals of 8 to 22 m in length with some skeletal characteristics attaining a high degree of development within the suborder (Romer, 1966).

The economic importance of whales is quite significant although various representatives are not of equal importance in this respect. Some whales are caught in large numbers every year (fin whales and sperm whales) while others are hunted only at random. Valuable edible and commercial products are obtained from almost all organs of the whale. Oil is rendered from the skin and bones (commercial and edible). The meat contains 20 to 26% protein and can be a source of diverse protein concentrates (frothing and emulsifying agents, substitutes for egg protein and deficient peptone for preparing nutrient media in microbiology) (Faingersh *et al.*, 1953). The pancreas of whales can be used to produce insulin (1 kg of pancreas contains from 1,000 IU in the blue whale to 3,000 in the sperm whale; Egorova, 1953) and commercial pancreatin (skin-softening agent; Bodrov *et al.*, 1958); the liver can be used to produce vitamin A (1 g of liver contains from 400 IU in the humpback whale to 5,800 in the sperm whale; Mrochkov, 1953), vitamin B₁₂, and campolon (Bodrov *et al.*, 1958). The brain of whales can serve as raw material for producing cholesterol (frozen brains of fin whale, blue whale, and humpback whale contain roughly 2.5% or about 11% of it in terms of dry matter; Egorova and Lebedeva, 1953).

The skin of whales, apart from providing fat, is useful as leather. The upper denser sections of the sperm whale are used to produce sole leather while the lower more porous ones are used as soft leathers (Zaikin, 1953). (V.S.)

431

Key to Suborders of Cetacea

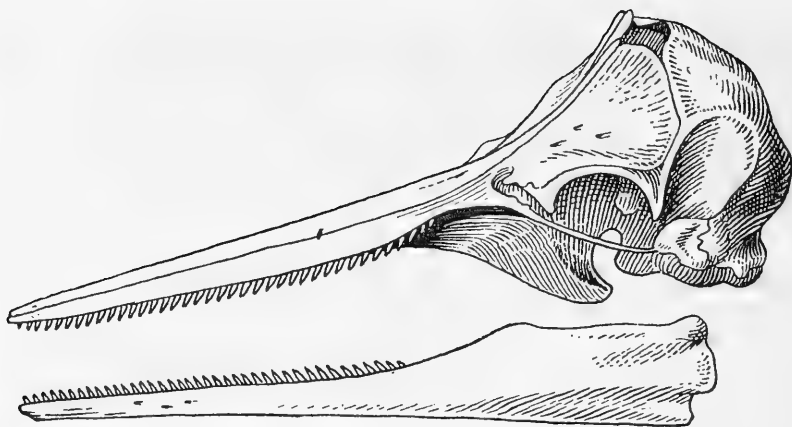
- 1 (2). Teeth absent. Numerous horny plates on upper jaw form straining apparatus. External nares bipartite. Skull symmetrical. Middle sections of movable halves of lower jaw flexed outward. Only first pair of ribs joined to sternum. . . . Suborder of baleen whales, Mysticeti.
- 2 (1). Teeth present. Straining apparatus absent. External nares not bipartite. Skull asymmetrical in frontal section. Middle sections of immovable halves of lower jaw straight or flexed inward. Not less than three pairs of ribs joined to sternum. Suborder of toothed whales, Odontoceti (See below).

432

SUBORDER OF TOOTHED WHALES

Suborder ODONTOCETI Flower, 1867

Size small, medium, and large (body length up to 2 m, up to 4 to 6 m, and up to 21 m). The body is torpedo- or teardrop-shaped.



432 Fig. 227. Skull of the common dolphin, *Delphinus delphis* (figure by N. N. Kondakov).

In the skin, the dermal layer and, in most cases, its fat-free portion are well distinguished. The network of elastin fibers is relatively poorly developed (except in small dolphins). A hair coat is lacking in most species. The body color is monochromatic, sometimes with typical white spots and bands.

The skull bones (Fig. 227) are sharply asymmetric although, in the early stages of embryogeny, the skull is characterized by all features characteristic of the skull of land mammals (Sleptsov, 1940). But this similarity disappears very soon as a result of the intense growth of the supraoccipital and premaxillary bones and also the supraorbital processes of the frontal bones, and the skull of the embryo then resembles that of an adult. Uneven development of the skull bones is also seen in the late stages of embryonic growth and extends into the postembryonic stage (Sleptsov, 1940c). The reasons for the genesis of asymmetry have not been accurately ascertained thus far: some researchers suggest that the unequal pressure of water on different sections of the skull while swimming is probably responsible while others regard this asymmetry as a consequence of the reduction of olfactory nerves. The nasal bones are poorly developed and do not cover the posterior part of the bony nares.

433 The nares are displaced leftward and open into a common chamber. Maxillae, premaxillae, and nasal bones are notably shifted onto the frontals and almost wholly cover them. Primitive features of structure are seen in the skull: presence of os parasphenoideum, tabularia, and postfrontalia; the number of bony components in the skull of embryos is more than in juvenile and adult animals (Sleptsov, 1949c). Cervical vertebrae may be

fused. Among the fast-swimming species, the number of caudal vertebrae is more. Among the deep-diving animals, because of the reduced number of ribs (in the sperm whale, their number decreases to three), the latter are joined to the sternum by flexible joints or attached by cartilage (beaked whales).

The dental formula varies from $\frac{0}{1}$ or $\frac{1}{0}$ to roughly $\frac{55}{55}$. The teeth are homodont and monophyodont. Three types of teeth are distinguished (Fig. 228) (Yablokov, 1958a):

1. Simple peg-shaped teeth with highly developed pulp cavity and thin cement and enamel layers among adult animals. This type of dental system is found in the common dolphin, common porpoise, pilot whale, etc. Except for the pilot whale, all these animals have a large number of teeth uniformly distributed in the jaws.
2. Teeth with highly developed layer of cement; enamel lacking on the teeth of adult animals; the tooth crown in the young animals has a thin layer of enamel (Lenberg, 1911). Teeth are simple, peg-shaped, larger than in the first type, and their number goes up to 30-50. The pulp cavity is well developed or absent. This tooth type is seen among sperm whales, white whale, apparently in dwarf sperm whale, Risso's dolphin, dwarf killer whale, Irrawaddy River dolphin, and false killer whale.
3. Teeth are flat, wedge-shaped, with highly developed enamel layer and cement filling the pulp cavity and thus covering the entire tooth with the exception of the crown; further, the cement layer typically adheres to the enamel layer in the midportion of the tooth. The number of teeth is small and they occur only in the lower jaw. This type is characteristic of Baird's beaked whale, beaked whales, and apparently the rest of the members of this family except for the Tasman beaked

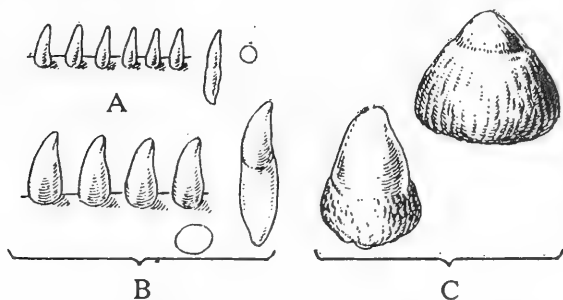


Fig. 228. Teeth of whales. A—common dolphin, *Delphinus delphis*; B—white whale, *Delphinapterus leucas*; C—Baird's beaked whale, *Berardius bairdi* (figure by N.N. Kondakov).

whale. The teeth of the killer whale occupy an intermediate position between the first and second types. They are similar to the teeth of the first type but differ from them in their large dimensions, comparatively small pulp cavity, and large amount of dentine. In these respects, they resemble the teeth of the second type but, in contrast to them, have a poorly developed cement layer.

- 434 In most of the toothed whales, the number of teeth is subject to individual variation. Among some species, teeth are fewer in the upper than in the lower jaw (Baird's beaked whale, sperm whale, Risso's dolphin, etc.); among others, on the contrary, the number of teeth in the upper and lower jaws is identical (narwhal, white whale, common porpoise, and black finless porpoise).

Annual layers are deposited on the teeth and the age of toothed whales can be determined by counting these layers in a section of a tooth. A unique feature of some cetaceans is that the left (rarely the right) upper tooth has transformed into a tusk, as seen in the narwhal males (less commonly, in females also), reaching a length of 2.7 m.

The digestive system among all the species is totally separated from the respiratory tract and has several characteristic features (Yablokov, 1958b). The tongue, unlike in land mammals, has a different structure and function. It is highly mobile and is covered with a thick sheath consisting of many layers of horny epithelium and a massive layer of connective tissue. The tongue positions the captured quarry in the oral cavity, pushes it into the gullet, and prevents water from entering. The soft palate is absent.

The initial sections of the digestive tract are covered inside with many layers of horny epithelium, which evidently protects the tract from damage by hard portions of food swallowed whole. The multichambered muscular stomach (Fig. 229) among species feeding predominantly on cephalopods (sperm whale and Baird's beaked whale) has a lining of glandular epithelium in the first section (Sleptsov, 1955). The subsequent sections of the stomach apparently take part in the process of absorbing the food; their structure is similar to that of the intestine. A cecum is lacking (seen in *Platanista*; Weber, 1927) and the intestinal sections are not distinctly separated from each other.

The relative length of the intestine varies markedly from species to species.

Ratio of length of intestine to body length
(Yablokov, 1958b)

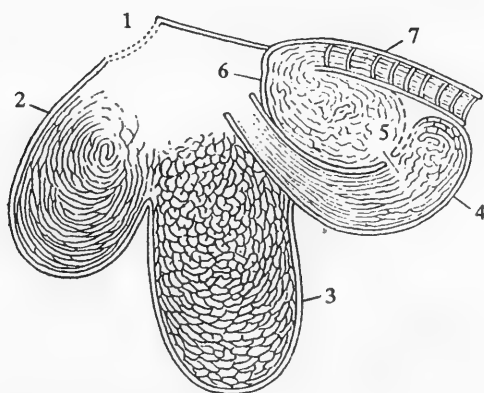
Bottlenose whale	1:6.0
Sperm whale	1:15.0 - 17.5

Common dolphin	1:10.4 - 12.5
Common porpoise	1:12.2 - 18.8
Bottlenose dolphin	1:14.4 - 15.8
Chinese finless porpoise	1:6.5
White whale	1:6.1 - 9.1

435 The respiratory system too reveals several characteristic features. The external nares are not bipartite (Fig. 230) and are supported by dense dermomuscular folds, such that the projections of one fall into the depression of the other. Several special paired air sacs lie above the skull: the upper ones dorsally, the lower ones proximally, the rear ones nasofrontally with additional cavities, and the lateral ones enterolaterally (Kleinenberg and Yablokov, 1958). Their function consists in supporting the nasal passage while diving; the greater the pressure of water, the more intense their action. Moreover, they produce sounds.

The larynx projects into the internal nares in the form of a tube formed by elongated arytenoid cartilages and the epiglottis (Fig. 231). This tube is covered by a special muscular sphincter. Bronchioles contain annular sphincters of smooth muscles (lacking in bottlenose whales). These are best developed in smaller species which dive often and thus breathe often and have a relatively large lung capacity.

Apparently, the system of sphincters enables adaptation to pressure changes in the lungs during frequent dives and powerful inhalation/exhalation (Slijper, 1958a).

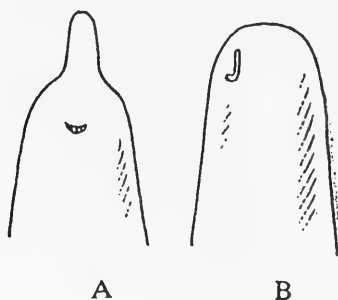


433 Fig. 229. Structure of the stomach of toothed whales (figure by N.N. Kondakov).
1—esophagus inlet; 2—first section of stomach; 3—second section of stomach; 4—third section of stomach; 5—sphincter; 6—duodenal ampule; 7—commencement of duodenum.

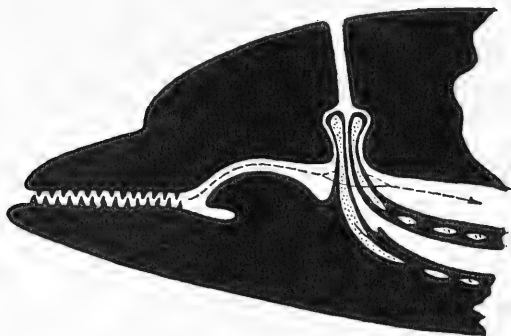
The brain has well-developed ventral nuclei in the auditory nerve, anterior olives, etc. (Ogawa and Arifuku, 1948). The auditory organ differs significantly from that of baleen whales in the shape of the tympanic bulla and the mode of its attachment to the skull (Yamada, 1953).

Sexual dimorphism is manifest among many species and is most distinctly seen in the dimensions of the animals: the males of most toothed whales are larger than the females. There are other differences too in some species. Thus, the dorsal fin among male killer whales is much higher than in females while a tusk is a feature of male narwhals (mainly).

In the course of postnatal development, changes occur in body dimensions and its sections. Some species undergo color changes too (for example, white whales which are dark colored at birth turn lighter and become white with advancing age).



434 Fig. 230. Unpaired blowhole among toothed whales, viewed from above (figure by N.N. Kondakov). A—bottlenose whale; B—sperm whale.



434 Fig. 231. Structure of the upper respiratory passages (figure by N.N. Kondakov).

Almost all toothed whales are fast swimmers, which has a bearing on their food characteristics. Some are capable of deep and prolonged submergence. They live on the coasts as well as in the open sea. Some are found in rivers and species of the family of river dolphins, Susuidae, regularly inhabit large rivers (Ganges and the Amazon). All the toothed whales, unlike baleen whales, swallow prey entire. Depending on the predominant food, several adaptive groups can be distinguished (Tomilin, 1957).

1. Ichthyophagous whales, feeding mainly on pelagic schools of fish. Their rostrum is long and narrow and the teeth numerous and covered with enamel. The common dolphin and dolphins of the genus *Stenella* belong to this group.

2. Benth-ichthyophagous whales consuming mainly bottom-dwelling fish and invertebrates. The rostrum is considerably shortened and the number of teeth less. Common porpoise, white dolphin, bottlenose dolphin, etc. belong to this group.

3. Teuthophagous whales, feeding mainly on cephalopods. These have a small number of teeth but none at all on the upper jaw. Sperm whale, beaked whales, bottlenose whale, etc. belong to this group.

4. Teutho-ichthyophagous whales (pilot whale and false killer whale), consuming cephalopods and fish. They occupy an intermediate position between the second and third groups. The rostrum is reduced in length, but broadened because of the premaxillae. Although the number of teeth is less, they are well developed.

5. Sarcophagous whales (killer whales), along with fish also feed on large marine mammals. They have short but massive jaws with few but very strong teeth.

Toothed whales are distributed in all the oceans, in almost all the open seas of the world, and in some rivers and lakes.

436 Among the primitive Odontoceti of family Agrophidae Abel, 1913 (Upper Eocene), the early stage of bone extension in the skull has been observed: the maxillae began extending posteriorly and covering the frontal bones while the nostrils occupied a position above the orbit. The members of Agrophidae apparently represent the ancestors of Squalodontidae Brandt, 1873 (Oligocene-Miocene) which in the Lower Miocene gave rise to contemporary dolphins (Delphinidae) and sperm whales (Physeteridae) and during the Miocene to beaked dolphins (Ziphiidae).

The systematics of the suborder of toothed whales has not been adequately studied, not only with respect to morphology and diagnosis of the species, but even the number and composition of the families.

Most scientists have no doubts about the correctness of recognizing river dolphins, beaked whales, and sperm whales as individual families (Kellogg, 1928; Nishiwaki, 1972 placed the dwarf sperm whale in the family Kogiidae). Views differ regarding the white whale and the narwhal, dolphins per se, and the common porpoise (for more details, see p. 586). Combining all the three above-mentioned groups of whales into two families is evidently more correct (Hershkovitz, 1966; Yablokov *et al.*, 1972). Thus the suborder of toothed whales includes three contemporary superfamilies and four families: river dolphins—Platanistoidea Simpson with one family of river dolphins, Platanistidae Gray (= Susuidae); dolphins—Delphinoidea Flower with two contemporary families: dolphins, Delphinidae Gray and narwhals, Monodontidae Gray; and sperm whales—Physeteroidea Gill with two families: sperm whales, Physeteridae Gray and beaked dolphins, Ziphiidae Gray (= Hyperoodontidae). The suborder comprises 31 genera and 71 species (Hershkovitz, 1966). In the USSR, the members of two superfamilies and three families (not river dolphins), 15 genera (roughly 48% of the world fauna) and 17 species (roughly 23%) are found (Tomilin, 1962).

The suborder includes five extinct families: Agrophiidae Abel (Upper Eocene of North America); Squalodontidae Brandt (Upper Oligocene-Upper Miocene of Europe, Lower Miocene of South America, Australia, and New Zealand, and Middle and Upper Miocene of North America); Eurhinodelphidae Abel (Lower Miocene of South America, Lower and Upper Miocene of Europe, Middle Miocene of North America, and Upper Miocene of Japan); Hemisyntrachelidae Slijper (Middle Miocene of North America and Lower Pliocene of Europe); and Acrodelphidae Abel (Lower and Upper Miocene of Europe and Middle Miocene and Lower Pliocene of North America).

Some toothed whales have acquired economic importance in the recent past. Sperm whales are even now caught in large numbers. At the same time, many of the scarce and less numerous species are practically of no importance.

Not all the species of toothed whales which could serve as valuable targets of hunting are caught in sufficient numbers in the waters of the USSR (for example, killer whales) and some are not caught at all (for example, dolphins in the waters of the Far East). (V.S.)

*Key to Species of the Suborder of Toothed Whales Inhabiting and
Probably Found in USSR Waters*

- 1 (6). Anterior part of snout strongly projecting beyond tip of lower jaw. Functional teeth absent or not more than three pairs in

- upper jaw and not less than seven pairs in lower jaw. Symphysis of lower jaw halves covers more than one-third their length.
- 2 (3). Body dimensions large (3-5 m in newborns and up to 15-21 m in adults). Head accounts for one-third body length. Blowhole at end of snout. Dorsal fin low, hump-shaped. Lower jaw with 18-28 pairs of massive teeth. First cervical vertebra free, remainder fused
.....Sperm whale, **Physeter catodon** (p. 801).
- 3 (2). Body dimensions small (not more than 4 m in adults). Head accounts for roughly one-fifth body length. Blowhole at center of head. Dorsal fin concave along posterior margin. Lower jaw with 9-16 pairs of small curved teeth. All cervical vertebrae fused.
- 4 (5). Body length 2.7-3.4 m. Lower jaw with 12-16 (less often, 10 or 11) pairs of teeth
.....Pygmy sperm whale, **Kogia breviceps** (p. 841).
- 5 (4). Body length 2.1-2.7 m. Lower jaw with 8-11 (less often, 13) pairs of teeth. ... Dwarf sperm whale, **Kogia simus** (p. 845).
- 6 (1). Anterior part of snout slightly projecting or not projecting beyond tip of lower jaw. Functional teeth present in both upper and lower jaws. If absent in upper jaw, their number in lower jaw does not exceed seven pairs. Symphysis of lower jaw halves does not exceed one-third their length.
- 7 (16). Teeth absent in upper jaw, not more than two pairs in lower jaw. One or two pairs of furrows on neck converging anteriorly. Notch not present on posterior edge of caudal flukes. Dorsal fin closer to flukes than to flippers.
- 8 (11). Width of midportion of straight, long, thin rostrum not less than one-seventh its length. Only one pair of teeth in lower jaw, located far behind anterior end of jaw. Teeth highly flattened laterally (their smaller diameter not less than one-half larger diameter). Fully developed tooth laterally trapezoid.
- 9 (10). In skull, antorbital notches relatively poorly developed. Aperture of pair V of nerves in maxilla anterior to aperture in premaxilla or at the same level. Palatine bones not contiguous. Ratio of length of tooth crown to width more than 6:1
.....Stejneger's beaked whale, **Mesoplodon stejnegeri** (p. 866).
- 10 (9). In skull, antorbital notches relatively well developed. Aperture of pair V of nerves in maxilla posterior to aperture in premaxilla. Palatine bones contiguous. Ratio of length of tooth crown to width not more than 4:1
.....Sowerby's beaked whale, **Mesoplodon bidens** (p. 869).

- 11 (8). Width of midportion of rostrum not more than one-sixth its length. Teeth located on anterior end of lower jaw and conical (larger diameter exceeds smaller by not more than 1.5 times).
- 12 (13). Length of head about 20% of body length. Massive crests running along maxillae reaching level of skull apex. Maximum diameter of anterior tooth usually not more than 2 cm Northern bottlenose whale, **Hyperoodon ampullatus** (p. 885).
- 13 (12). Length of head about 13-17% of body length. Low crests running along maxillae not reaching level of skull apex. Maximum diameter of anterior tooth does not exceed 2 cm.
- 438- 14 (15). Two pairs of teeth present. "Beak" flattened dorsoventrally. Rostrum from above not triangular Baird's beaked whale, **Berardius bairdii** (p. 850).
- 15 (14). One pair of teeth present. "Beak" not flattened dorsoventrally. Rostrum from above triangular Cuvier's beaked whale, **Ziphius cavirostris** (p. 876).
- 16 (7). In most species, teeth present in upper and lower jaws. Teeth absent in upper jaw only in Risso's dolphin, and in lower jaw in narwhals. In latter case, however, width of midportion of rostrum $2/5 - 1/3$ its length. Furrows not visible on neck. Notch present between caudal flukes.
- 17 (26). Dorsal fin lacking.
- 18 (23). Head rounded, without "beak".
- 19 (22). Number of teeth not more than 44. Neck distinctly visible. Horny protuberances absent on dorsum.
- 20 (21). Body monochromatic (white or yellow in adults). Up to 44 teeth in upper and lower jaws White whale, **Delphinapterus leucas** (p. 757).
- 21 (20). Body of adult animals spotted (monochromatic, dark, in juveniles). Teeth lacking or not more than one pair on upper jaw. In males and sometimes in females, left upper tooth in form of spirally twisted tusk Narwhal, **Monodon monoceros** (p. 791).
- 22 (19). Number of teeth up to 100. Neck lacking. Horny protuberances present on dorsum Black finless porpoise, **Neophocaena phocaenoides** (p. 750).
- 23 (18). "Beak" well developed. Number of teeth exceeds 160.
- 24 (25). Entire body black, with narrow light-colored band only along abdomen from neck to tail; band forms rhomboidal patch on

- breast
- .. Northern right whale dolphin *Lissodelphis borealis* (p. 646).
- 25 (24). Body black except for white lower sections and abdominal flanks
 .. Southern right whale dolphin, *Lissodelphis peroni* (p. 651).
- 26 (17). Dorsal fin present.
- 27 (42). "Beak" absent or barely perceptible.
- 28 (29). Body length exceeds 4 m. Flippers broad (length not more than twice width) and rounded. Teeth massive (diameter more than 2.5-2.8 cm). Body dark in color. White band on abdomen extending as tongue on flanks in region of anal opening, its tip directed anteriorly. Dorsal fin high, especially in males (up to 1.7 m) Killer whale, *Orcinus orca* (p. 680).
- 29 (28). Body length less than 4 m; if more, flippers narrow (length exceeds width by more than 2.5 times) and pointed. Tooth diameter not more than 2.5-2.8 cm. Body color different. Dorsal fin smaller.
- 30 (31). Teeth absent in upper jaw (sometimes one or two pairs seen); two to seven pairs present in lower jaw
 Risso's dolphin, *Grampus griseus* (p. 696).
- 31 (30). More than six pairs of teeth in upper jaw and more than seven pairs in lower jaw.
- 32 (37). Teeth in upper and lower jaws not more than 8-13 pairs each.
- 33 (34). Low dorsal fin in anterior half of body. Head anteriorly obtuse with high forehead. Teeth only in anterior half of upper jaw Pilot whale, *Globicephala melaena* (p. 702).
- 439 34 (33). Relatively high dorsal fin roughly midbody. Head anteriorly rounded. Teeth in upper jaw not exclusively in anterior half.
- 35 (36). Entire body black. Roughly 50-51 vertebrae
 False killer whale, *Pseudorca crassidens* (p. 674).
- 36 (35). Body dark gray, edge of jaws and region around anal opening white. Roughly 67-70 vertebrae
 Dwarf killer whale, *Feresa attenuata* (p. 719).
- 37 (32). Teeth in upper and lower jaws more than 15 pairs each.
- 38 (39). Body size of adult animals exceeds 2 m
 Broadsnout dolphin (melon-headed whale),
Lagenorhynchus electra (p. 672).
- 39 (38). Body size of adult animals exceeds 2 m.
- 40 (41). Dorsal side of caudal crest with high keel. White field on body flanks sharply set off from surrounding dark background.

- Number of teeth in upper jaw (15-24 pairs) usually less than in lower (22-28 pairs) Dall porpoise, **Phocoenoides dalli** (p. 738).
- 41 (40). High keel on dorsal side of caudal crest lacking. Body color different. Number of teeth in upper jaw (16-30 pairs) usually more than in lower jaw (16-27 pairs) Common porpoise, **Phocoena phocoena** (p. 722).
- 42 (27). "Beak" distinctly perceptible.
- 43 (44). Symphysis of lower jaw more than one-fourth its length. Tooth crowns grooved Rough-toothed dolphin, **Steno bredanensis** (p. 591).
- 44 (43). Symphysis of lower jaw less than one-fourth its length. Tooth crowns smooth.
- 45 (52). "Beak" of moderate length or short. Body length exceeds "beak" length (from tip of snout to beginning of corpus adiposum) by more than 25 times. Diameter of teeth in middle of tooth row exceeds 3 mm.
- 46 (47). Teeth not more than 20 pairs in upper jaw and 26 pairs in lower. Diameter of teeth in middle of tooth row exceeds 6 mm. "Beak" dark in color. Keel absent on dorsal side of caudal crest Bottlenose dolphin, **Tursiops truncatus** (p. 632).
- 47 (46). More than 26 pairs of teeth each in upper and lower jaws. Diameter of teeth in middle of tooth row less than 6 mm. If number of teeth less (up to 22 pairs), their diameter more (up to 7 mm). Beak white. Keel present on dorsal side of caudal crest.
- 48 (49). Tip of "beak" white. Trunk dark-colored above right up to joint with flippers. Number of vertebrae exceeds 84. Number of teeth in upper and lower jaws less than 28 pairs. Pterygoid bones separated by gap, broadened anteriorly White-beaked dolphin, **Lagenorhynchus albirostris** (p. 660).
- 49 (48). Tip of "beak" dark. Dark color of trunk does not descend to joint with flippers. Number of vertebrae less than 84. Number of teeth in upper and lower jaws more than 28 pairs. Pterygoid bones adjacent or separated by gap, not broadened anteriorly.
- 50 (51). Number of vertebrae 74-78; ribs 12-14 pairs; teeth in upper jaw usually 30-32 pairs. Narrow dark band extending along body flanks from base of flippers to lower caudal crest Pacific white-sided dolphin, **Lagenorhynchus obliquidens** (p. 664).
- 440 51 (50). Number of vertebrae 77-82. Ribs 14-15 pairs. Teeth in upper jaw usually 35-38 pairs. Dark band along body flanks from base

- of flippers to lower caudal crest absent
 Atlantic white-sided dolphin, *Lagenorhynchus acutus* (p. 656).
- 52 (45). "Beak" long. Body length exceeds "beak" length (from tip of snout to beginning of corpus adiposum) by not more than 20 times. Diameter of teeth in middle of tooth row not more than 3 mm.
- 53 (54). Dark band extending from flippers to chin. Palate with two longitudinal grooves
 Common dolphin, *Delphinus delphis* (p. 607).
- 54 (53). Dark band extending from flippers to chin absent. Palate without grooves.
- 55 (56). Body dark gray above, white below. Length of rostrum of skull twice length of cerebral section. Number of teeth $\frac{46-56}{46-56}$
 .. Long snout [spinner] dolphin, *Stenella longirostris* (p. 604).
- 56 (55). Body black or blackish above, white, whitish, or ash-gray below. Length of rostrum less than twice length of cerebral section. Number of teeth $\frac{35-50}{35-50}$.
- 57 (58). Body black above, white below. Number of teeth $\frac{44-50}{44-50}$
 .. Blue-white [striped] dolphin, *Stenella coeruleoalba* (p. 594).
- 58 (57). Body blackish above, whitish or ash-gray below. Number of teeth $\frac{35-44}{35-44}$.
- 59 (60). Body ash-gray below. Maxillary teeth small, less than 3 mm in diameter. Number of vertebrae 79-81
 Malay [Pan-Tropical spotted] dolphin, *Stenella dubia* [= *attenuala*] (p. 601).
- 60 (59). Body whitish below. Maxillary teeth large, more than 5 mm in diameter. Number of vertebrae not more than 70
 Bridled dolphin [Atlantic spotted dolphin],
Stenella frontalis (p. 602). (V.S.)

SUPERFAMILY OF DOLPHINS

Superfamily DELPHINOIDEA Flower, 1864

Cetaceans of small and medium dimensions.

The body of most of the dolphins is well proportioned. The caudal fin bears a deep notch between the flukes. Many species have a large dorsal fin (sometimes lacking) in the midbody. Furrows not seen on the neck. Rostral part of head stretched into a well-distinguishable "beak" which, however, may be poorly developed or altogether absent. The "beak" may

be sharply demarcated from the frontal portion of the head or may pass smoothly into it. The body is monochromatic (dark or light in color) or dark above and light-colored below, or dark with light-colored bands that vary in disposition, shape, and number.

The zygomatic and temporal bones are poorly developed in the skull. The supraoccipital and frontal bones overhang a small temporal fossa. Crests are lacking on the maxillae. The pterygoid and nasal bones are relatively small. The palatine bones are joined along the midline of the palate and are not separated from the vomer. The zygomatic process of the squamosal bone is highly reduced.

- 441 The symphysis of the lower jaw is not more than one-third the jaw length. The width (spacing) of the lower and upper jaws is nearly similar. The number of teeth varies from $\frac{65}{58}$ to $\frac{0}{2}$.

These are migratory animals living in schools. Their food is diverse: fish (ichthyophagous whales), cephalopod mollusks (teuthophagous), cephalopods and fish (teutho-ichthyophagous), and warm-blooded vertebrates (sarcophagous).

The species of the superfamily live in almost all the seas of the world right up to the icy seas in the high Arctic. Some are very widely distributed, almost throughout the world (common dolphin and killer whale) while others are more localized. Some species (genus *Sotalia*) live in rivers (South America and southern Asia).

Members of the family are known from the Lower Miocene, having separated from the ancient Squalodontidae. The oldest members (*Argyrocetus*, *Schizodelphis*, and *Delphinavus*) had a long and narrow rostrum and a large number of teeth. The contemporary form of the dolphin can be traced to the end of the Miocene-Early Pliocene.

The systematics of dolphins has been differently interpreted by various scientists.

In the superfamily of dolphins, Delphinoidea, one family—Delphinidae (Tomilin, 1957), two families—Delphinidae and Monodontidae (Hershkovitz, 1966; Yablokov *et al.*, 1972), or three families—Monodontidae, Delphinidae, and Phocoenidae (Simpson, 1945) have been distinguished. In more detailed systems, the number of families has risen to four—Monodontidae, Stenidae, Phocoenidae, and Delphinidae (Andersen and Jones, 1967), or even six—Monodontidae, Delphinidae, Grampidae, Globicephalidae, Orcaelidae, and Phocoenidae (Nishiwaki, 1966; Ridgway, 1972).

It would appear to be more correct to combine all these groups into two families: dolphins (Delphinidae) and narwhals (Monodontidae).

Representatives of both the families are found in the USSR fauna. The extinct forms are represented in the superfamily of dolphins by the family Eurinodelphinidae (three genera), family Hemisyntrachelidae (two genera), and family Acrodelphidae (six genera). Moreover, 24 genera belong to the family Delphinidae (Simpson, 1945).

Some representatives of the family are of economic importance and are hunted in large numbers. Others are almost not caught because of their small number or for other reasons and have no economic importance. (V.S)

Family of Dolphins

Family DELPHINIDAE Gray, 1821

Animals of small, medium, and large dimensions.

The dorsal fin in most cases is well developed. There is no neck between the head and the trunk.

The rostrum of the skull is usually longer than the cranium. The petrous temporal bone does not grow toward the skull but is attached to it by ligaments. The cervical vertebrae may be fused (atlas and axis more often fused). The anterior ribs have a double articulation with the vertebrae. The ulnar process is well developed in the forelimb.

Open seas, coastal zone, and rivers are inhabited.

The geographic distribution of the members of the family covers the range of the superfamily; only the northern limit falls more southward.

442 The family comprises 18 genera,¹ of which 14 have been reported (or may still be found) in USSR waters: rough-toothed dolphins, *Steno* Gray; spotted dolphins, *Stenella* Gray; common dolphins, *Delphinus* Linnaeus; bottlenose dolphins, *Tursiops* Gervais; right whale dolphins, *Lissodelphis* Gloger; shorthead dolphins, *Lagenorhynchus* Gray; false killer whales, *Pseudorca* Reinhardt; killer whales, *Orcinus* Fitzinger; Risso's dolphins, *Grampus* Gray; pilot whales, *Globicephala* Lesson; dwarf killer whales, *Feresa* Gray; common porpoises, *Phocoena* G. Cuvier; Dall porpoises, *Phocoenoides* Andrews; and black finless porpoises, *Neophocaena* Palmer. The remaining four genera inhabit waters outside the USSR: *Sotalia* Gray, *Lagenodelphis* Fraser, *Cephalorhynchus* Gray, and *Orcaella* Gray.

The species of some genera are of economic importance. (V.S.)

¹ According to P. Hershkovitz (1966), the placement of *Lagenorhynchus electra* Gray in an independent genus, *Peponocephala* Nishiwaki and Norris (*Electra* auct.—nom. praeocc.), requires further justification.

Genus of Rough-toothed Dolphins

Genus *Steno* Gray, 1846

1846. *Steno*. Gray. Zoology Voyage Erebus and Terror. I, p. 30. *Delphinus rostratus* Cuvier = *Steno bredanensis* Lesson, 1828. (V.H.)

Small dolphins reaching up to 2.5 m in length (Fig. 232).

The "beak" on the head passes smoothly into the slope of the forehead. The dorsal fin is triangular, high, with a notch along the posterior edge [falcate].

The body is dark gray on the dorsum, light gray with yellowish-white spots on the flanks, and white on the abdomen.

The rostrum is long and narrow (Fig. 233), its length more than three times its width. The symphysis of the lower jaw constitutes over 30% of its length. The pterygoid bones are adjacent. The postorbital processes of the frontal bone are small. The teeth are large, with grooved crowns.

Teeth $\frac{20-27}{20-27}$ (usually $\frac{24}{24}$).

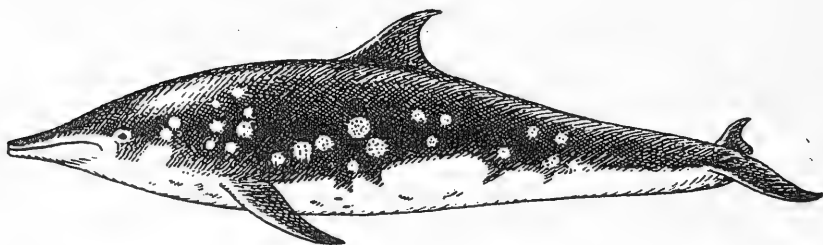
Vertebrae 65-66. The first and second vertebrae are fused.

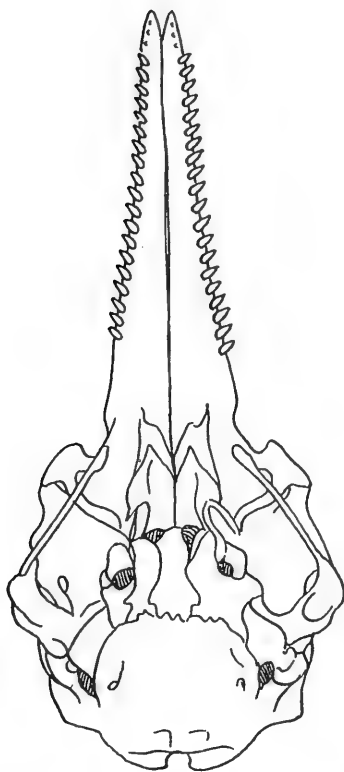
The biology of the dolphins of this genus is almost unstudied. Their population is insignificant. They live in groups and feed on squids and fish.

The geographic range covers the temperate and warm waters of the Atlantic and Pacific oceans and also the Indian Ocean. They have not been reported in the waters of the USSR. However, they might be found in the region of Kuril Islands and the Sea of Japan.

444 The genus comprises one species: the rough-toothed dolphin, *S. bredanensis* Lesson, 1828.

Sometimes the rough-toothed dolphin, together with the genera *Sotalia* Gray and *Sousa* Gray, is placed in a separate family, Stenidae Fraser and Purves, 1960 (Anderson and Jones, 1967). (V.S.)





442 Fig. 233. Skull of rough-toothed dolphin, *Steno bredanensis* (figure by N.N. Kondakov).

ROUGH-TOOTHED DOLPHIN²

Steno bredanensis Lesson, 1828

1817. *Delphinus rostratus*. Desmarest. Nouv. Dict. Hist. Nat., 9, p. 160. Bretagne, France. Nom. praeocc.
 1823. *Delphinus frontatus*. G. Cuvier. Rech. ossements foss., 5, p. 278. Portugal. Description does not conform to the rules of nomenclature.
 1828. *Delphinus bredanensis*. Lesson. Hist. Nat. mamm. oiseaux decon-verbés depuis 1788. Substituted for *Delphinus rostratus* Desmarest, 1817. (V.H.).

Single species of the genus. The body is well proportioned. The "beak" is somewhat compressed laterally. The dorsal fin lies roughly midbody. The flippers are broad at the base.

² Russian name corresponds to the English name. (V.H.)

A sharp demarcation of different colors is a characteristic feature of body coloration. The snout is sometimes white.

The adult male measures 2.23 m in length and weighs 102 kg. (V.S.)

Transgressions and habitation in our waters of the Sea of Japan and near the Kuril Islands are possible (Fig. 234).

Outside the USSR, this dolphin is found in the Pacific Ocean south of the strip Japan—Hawaiian Islands—California; in the Atlantic Ocean from the southern part of the North Sea (Holland) and waters of France in the east and Virginia in the west to roughly 40° S lat. (Tristan da Cunha, Argentina); and in the Indian Ocean from the northern coasts and Java to the Cape of Good Hope.

Geographic variability has not been established.

Biology not known. Lives in small schools. (V.H.)

Genus of Spotted Dolphins

Genus *Stenella* Gray, 1866

1864. *Clymene*. Gray. Proc. Zool. Soc. London, p. 237. *Delphinus euphrosyne* Gray, 1846. Nom. Praeocc.

1866. *Stenella*. Gray. Proc. Zool. Soc. London, p. 214. *Steno attenuatus* Gray, 1846.

1866. *Euphrosyne*. Gray. Ibid., p. 214. *Clymene euphrosyne* Gray. Nom. praeocc.

1880. *Prodelphinus*. Gervais. In: Van Bénédén et Gervais. Ostéographie des Cétacées, p. 604. Substituted for *Clymenia* Gray, 1864. (V.H.)

Small dolphins; body length up to 2.7 m.

The body is well proportioned. The dorsal fin is located midbody and its apex curved backward. The flippers are crescent-shaped. The "beak" is long and narrow. The lower jaw is slightly longer than the upper.

The body coloration differs markedly from species to species and, further, is subject to considerable individual variation. The dorsum and upper sections of the body flanks are usually dark; the lower portion of the body flanks and abdomen are light in color.

The premaxillae are curved in the rostral part of the skull. The pterygoid bones are adjacent. Longitudinal grooves are absent or very small on the palate. The symphysis of the lower jaw constitutes less than one-fifth the length of the jaw itself. The teeth are small, sharp, and 34–65 in each half of the jaw.

The cerebral section of the skull is broad in the occipital region and flat in the frontal region. The structural features of the skull of the
446 spotted dolphins on the one hand are similar to the common dolphins, *Delphinus*, and on the other to the genus of bottlenose dolphins, *Tursiops*.

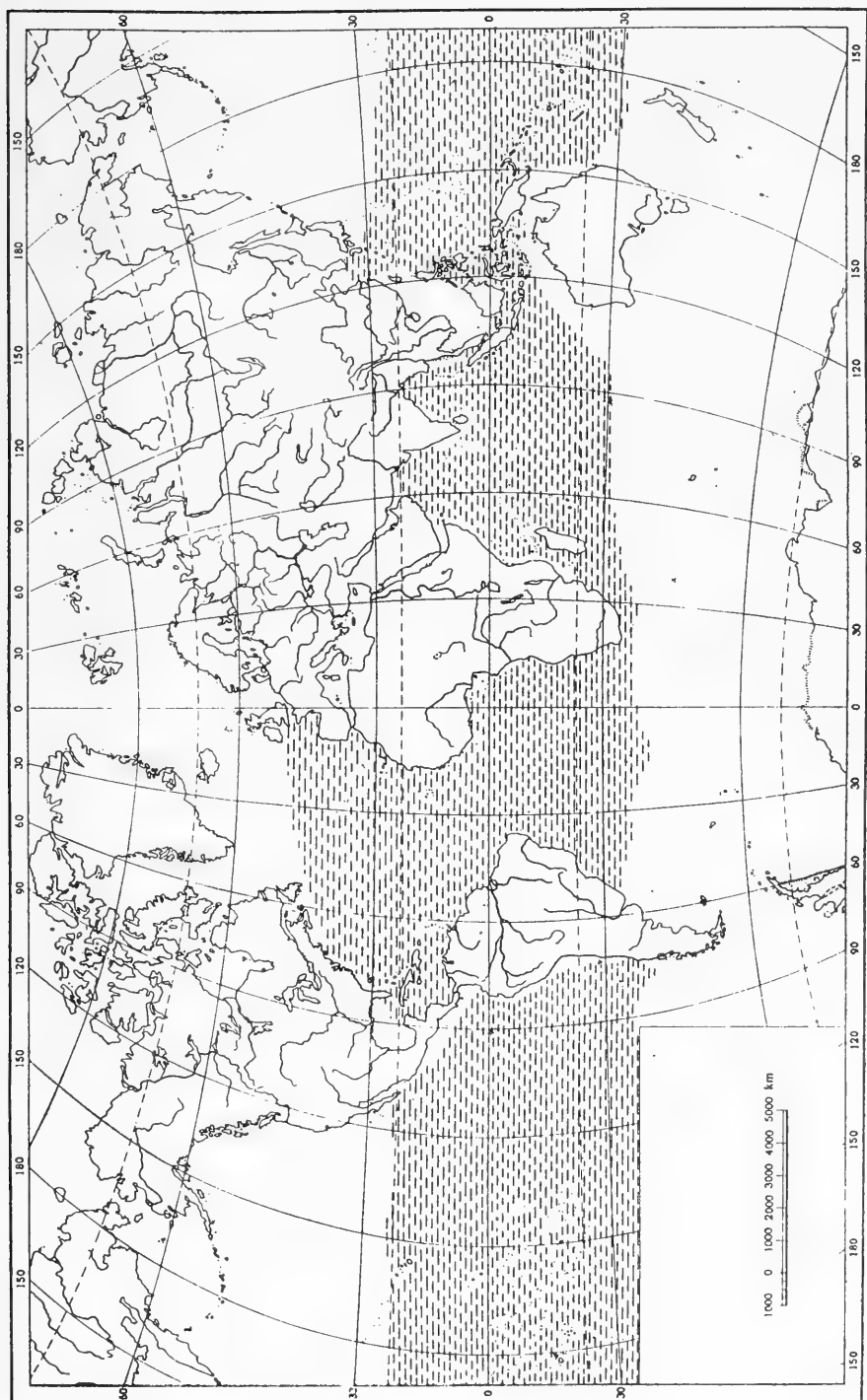


Fig. 234. Range of rough-toothed dolphin, *Steno bredanensis* (V.A. Arsen'ev).

The common features of spotted dolphins and common dolphins are the long rostrum, slightly exceeding the cerebral section of the skull, the large number of very small teeth, and premaxillae usually confluent with the rostral part of the skull. However, as in bottlenose dolphins, spotted dolphins do not have longitudinal grooves on the bony palate.

Long, thin, spinous and transverse processes are characteristic of the vertebrae. The cervical vertebrae may be fused. The sternum is T-shaped and consists of four sections. Ribs 15 - 16 pairs. In the flippers, the second and third digits are the longest (2nd one longer).

Biology almost not known.

Its distribution (Fig. 235) ranges from the cold to the tropical waters of the Pacific and Atlantic oceans (including the Mediterranean Sea), from the Bering Sea and Greenland to the Cape of Good Hope, Cape Horn, and Australia, and the Indian Ocean. Not caught in our waters.

The composition and systematics of species of the genus have not been adequately studied. Ten species are usually recognized but their number seems to have decreased: (1) *S. asthenops* Cope, (2) *S. clymene* Gray, (3) *S. coeruleoalba* Meyen, (4) *S. crotaphiscus* Cope, (5) *S. dubia* G. Cuvier, (6) *S. frontalis* G. Cuvier, (7) *S. graffmani* Lönnberg, (8) *S. longirostris* Gray, (9) *S. malayana* Lesson, and (10) *S. pernettyi* Blainville.³

Only the blue-white dolphin, *S. coeruleoalba*, is encountered in the waters of the USSR while the appearance or residence of *S. dubia*, *S. frontalis*, and *S. longirostris* is possible. (V.S.)

BLUE-WHITE [STRIPED] DOLPHIN

Stenella coeruleoalba Meyen, 1833

- 1833. *Delphinus coeruleo-albus*. Meyen. Nova. Acta Leop.-Carol., 16, 2, p. 609. Near La Plata estuary.
- 1846. *Delphinus styx*. Gray. Zoology Voyage Erebus and Terror, 1, p. 39. Atlantic Ocean around South Africa.
- 1846. *Delphinus euphrosyne*. Gray. Ibid., p. 40. North Atlantic, waters of England.
- 1848. *Delphinus lateralis*. Peale. U. S. Explor. Exped., Mammalia, p. 34. Pacific Ocean at 13°58' N lat. and 161°22' W long. (V.H.)

Diagnosis

Body length up to 260 cm. The dorsal surface is black and the ventral surface white. A narrow black band runs from the eyes to the anal opening

³ In alphabetical order, after Hershkovitz (1966).

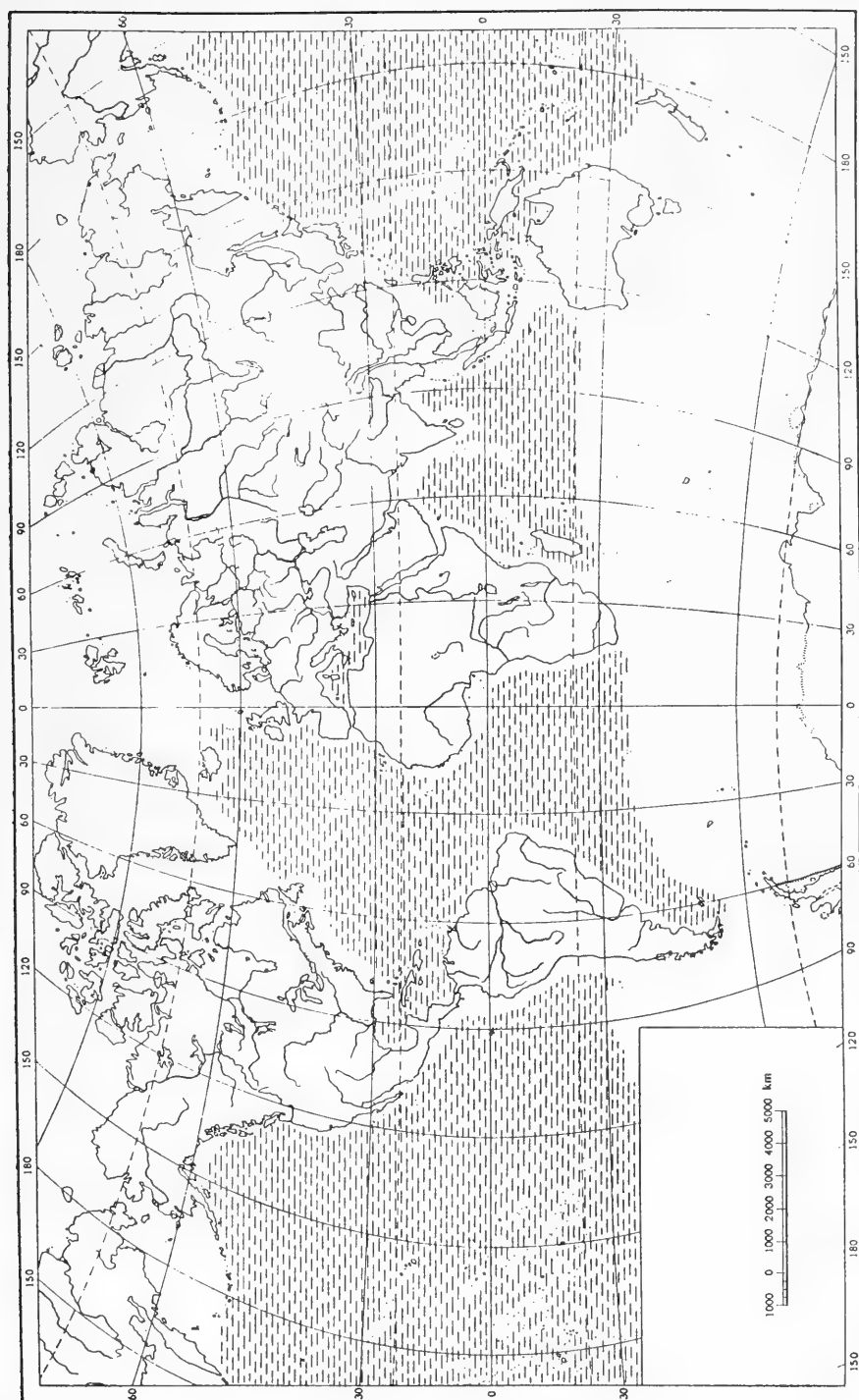


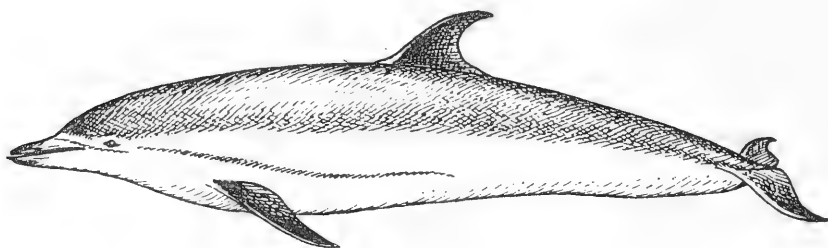
Fig. 235. Range of spotted dolphins, *Stenella* (V.A. Arsen'ev).

and from the eyes to the base of the flippers. The flippers are small. The length of the rostrum is less than double the length of the cerebral section of the skull. Teeth $\frac{44-50}{44-50}$. Vertebrae about 76-79. (V.S.)

Description

447 The main body measurements of female and male blue-white dolphins (Fig. 236) caught in the waters of Japan (Tomilin, 1957) are respectively (in cm): body length 200 and 196 (may go up to 2.7 m); distance from tip of snout to base of flippers 48 and 50, up to blowhole 34 and 35, up to anterior edge of dorsal fin 93 and 94, and up to anal opening 137 and 138; height of dorsal fin 17 and 15, length of the base of dorsal fin 31 and 28; width of caudal flukes 67 and 44; and length of flippers 27.

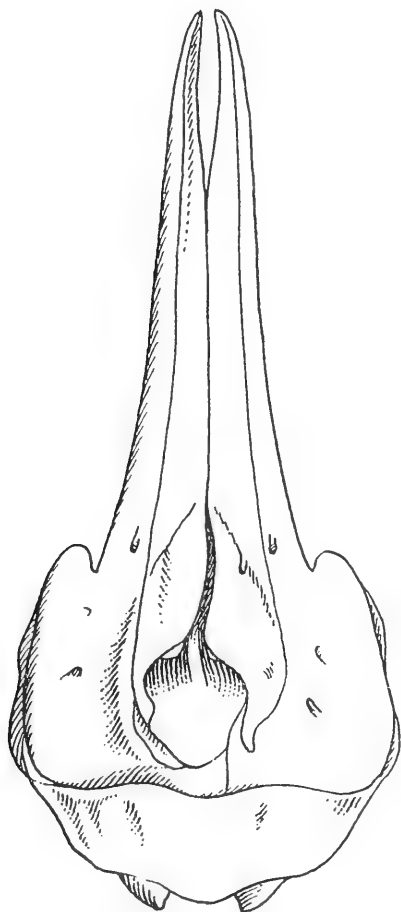
Of the more than 3,000 blue-white dolphins caught at the end of November, 1967 at village Kawana (Honshu Island), a random sample of 75 adults (body length 170 to 256 cm) comprised 59 females and 16 males; 71 newborn calves (body length 97 to 144 cm) comprised 36 females and 35 males (Sokolov and Kasupa, 1969). Among the females studied, six with a body length ranging from 184 to 217 cm (184, 199, 206, 208, 213, and 217) were immature; two with a body length of 139 [sic.] and 213 cm had not given birth before but were ready for fertilization (with large follicles in the ovaries); and nine had calved before (they bore traces of the corpus luteum of pregnancy in the ovaries) but were now barren or had lost their calves. The body length of these last nine females was: 217 cm (two), 224, 226 (two), 229, 231, 232, and 239 cm. The ovaries of two of them (body length 232 and 239 cm) contained large follicles. Of the remainder, 40 females were lactating (the status of two females could not be ascertained) and the ovaries of three contained mature follicles. The body length of these 40 females was (in cm): 209, 216 (two), 218 (two), 219, 221 (three), 222, 223 (four), 224 (four),



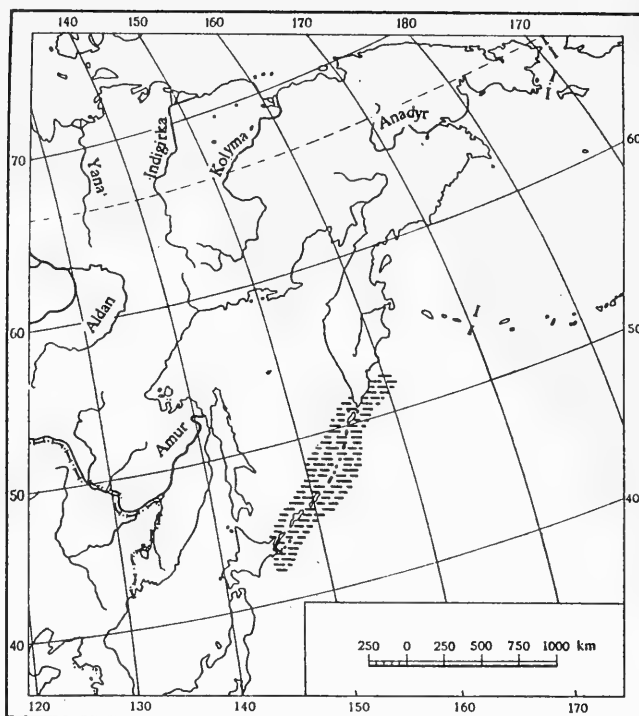
225, 226 (four), 227 (three), 228 (two), 229 (three), 230, 231 (three), 232 (two), 233, and 234 (two).

The body length of immature males varied from 170 to 214 cm (170, 176, 184, 191, 195, and 214 cm) and of mature males from 224 to 256 cm: 224, 228, 232 (two), 233, 235, 237, 239, 241, and 256.

The condylobasal length of the skull (Fig. 237) of these dolphins
448 from La Mancha was (in cm): 47, length of rostrum 29, width of rostrum at base 12, length of lower jaw 41, and length of symphysis of lower jaw 4 (Tomilin, 1957). Phalangeal formula: I_1 , II_{9-10} , III_7 , IV_4 , and V_{1-2} (V.S.)



447 Fig. 237. Skull of the blue-white dolphin, *Stenella coeruleoalba* (figure by N.N. Kondakov).



448 Fig. 238. Range of the blue-white dolphin *Stenella coeruleoalba* in the USSR (V.A. Arsen'ev).

Geographic Distribution

This dolphin inhabits the warm and temperate belts of the Atlantic and Pacific oceans. Studies of its distribution are highly schematic.

Geographic Range in the USSR

Waters of the Pacific Ocean around the Kuril Islands and possibly the waters of the Bering Sea (Fig. 238).

Geographic Range outside the USSR (Fig. 239)

Strays in the Atlantic Ocean northward up to the coasts of Great Britain, Shetland and Orkney Islands, and southern Greenland; known in the waters of Quebec and Nova Scotia. Not reported in the Northern, Baltic,

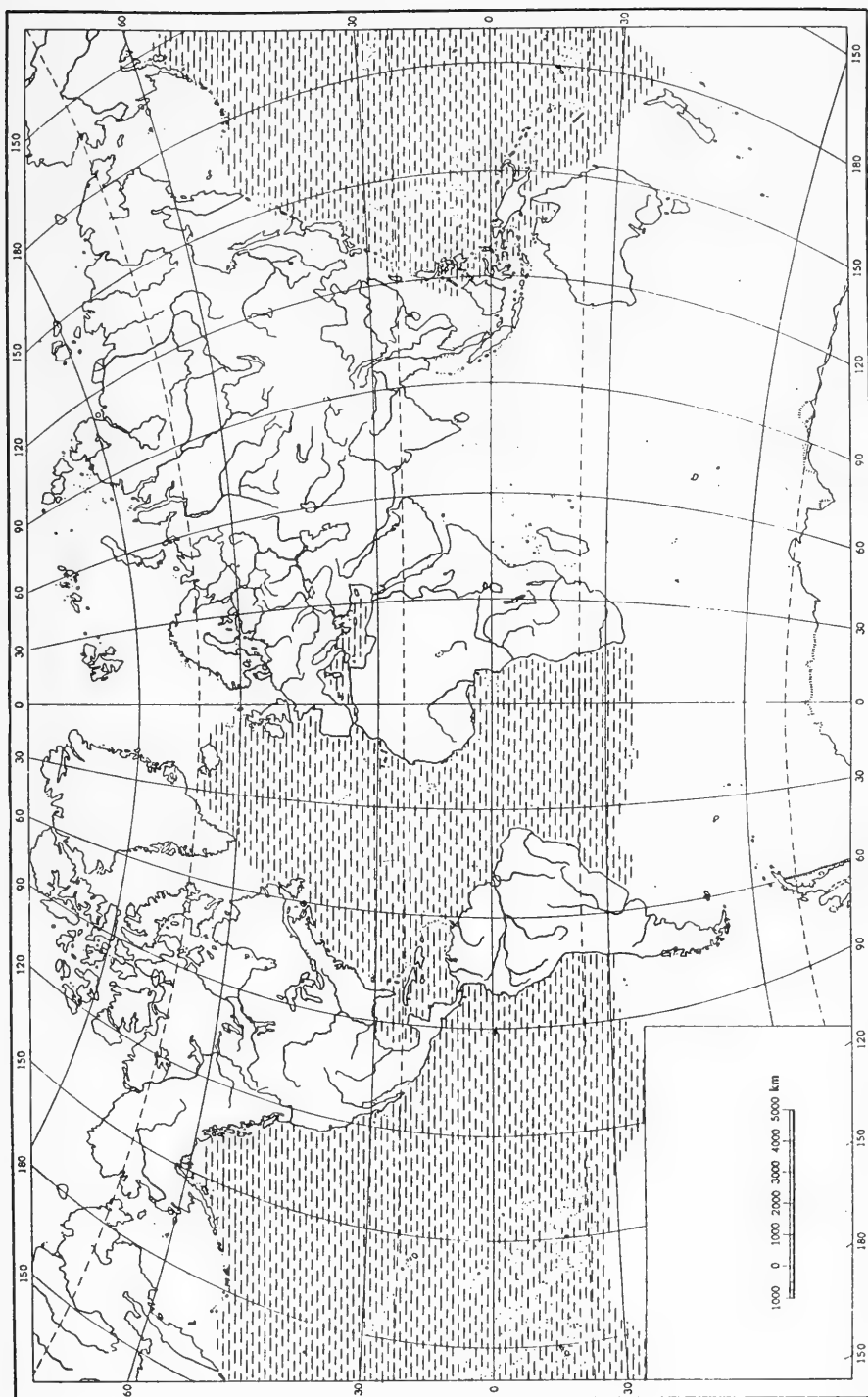


Fig. 239. Species range of the blue-white dolphin, *Stenella coeruleoalba* (V.A. Arsen'ev).

or Barents seas.⁴ Distributed southward up to Rio de La Plata along the South American coast and up to the southern tip of Africa. Lives in the Mediterranean Sea. In the Pacific Ocean, known from the coasts of Japan and the Kuril Islands in the west and from the Bering Sea, British Columbia, states of Oregon and Washington in the east up to New Zealand. [sic.] (V.A.)

Geographic Variation

Our knowledge of the geographic variation of the blue-white dolphin is extremely scant and this aspect has generally not been discussed in the world literature. In our literature on the fauna of the USSR, the existence of two subspecies is sometimes acknowledged (Tomilin, 1957, 1962). These are: the nominal form in the seas of the Far East and the Atlantic form, *S. c. euphrosyne* Gray, 1946, for "the Baltic Sea, possibly the Barents Sea". The main difference between them, in addition to some skull features, lies in coloration (band from eyes to base of flippers single in the former and double in the latter). Sometimes these two forms are treated as independent species. Their nomenclature differs according to different authors.

As pointed out above (see "Geographic Distribution"), the existence of the Atlantic form (*euphrosyne*) in our waters is just not possible. According to the convention prevailing in our literature, the name *S. c. coeruleoalbus* Meyen, 1833 may be retained only tentatively for the blue-white dolphin found in our Far Eastern waters. However, it would be better to use the binary name. It is quite possible that the use of the name *styx* Gray, 1846 might be more correct.

The systematics and nomenclature of the species and forms of the genus *Stenella* are complex and in a high state of confusion (compare, for example: Ellerman and Morrison-Scott, 1951, 1962; Tomilin, 1957, 1962; Hall and Kelson, 1959; Hershkovitz, 1966; and others). A radical review of the subject, based on substantial evidence, is required. (V.H.)

Biology

The biology of the blue-white dolphin has almost not been studied and practically no observations have been made on the behaviour of these animals at sea.

⁴ Information and assumptions on habitation in these seas (Tomilin, 1957, 1962) have not been confirmed in the latest compilations (Ellerman and Morrison-Scott, 1951, 1966; von den Brink, 1958; Koval'skii, 1964; Bobrinskii *et al.*, 1965; Hershkovitz, 1966; Siivonen, 1967). (V.H.)

The largest of the measured embryos was 103 cm long. All the young dolphins 120-150 cm long were comparatively recently born since their stomach contained exclusively milk or milk together with small quantities of the remnants of squids. The smallest female with a corpus luteum in the ovary measured 215 cm in length; apparently females of this size attain maturity. Among animals of this length (or slightly larger), the ovaries and testes begin to lengthen rapidly. Among dolphins caught in November, 1956, 12 were immature females, 72 gestating, and 27 simultaneously gestating and lactating. The oldest of these dolphins was 18 years of age (Nishiwaki and Yagi, 1953).

Sufficient numbers of the blue-white dolphin are caught in the coastal waters of some regions of Japan and China. Hunting is done in small crafts and with small-bore harpoon guns. The kill is sold in fish markets. Economic importance is very negligible. (V.A.)

MALAY [PAN-TROPICAL SPOTTED] DOLPHIN

Stenella dubia [= *attenuata*] G. Cuvier, 1812

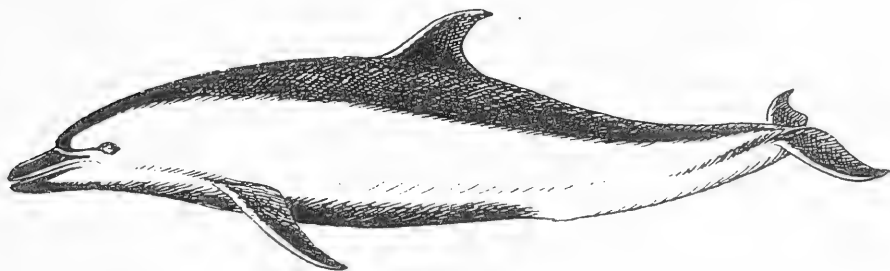
1812. *Delphinus dubius*. G. Cuvier. Ann. Mus. Hist. Nat., Paris, 19, p. 9. French waters. [nomen dubium]

1826. *Delphinus malayanus*. Lesson. Voyage autour du monde..., Zoologie, I, p. 184. South China Sea, strait between Java and Kalimantan (Borneo). [nomen dubium]

451 1846. *Steno attenuatus*. Gray. Zoology Voyage Erebus and Terror, I, p. 44. Type locality not established. (V.H.)

Body length up to 183 cm. The color is blackish above and ash-gray below (including the caudal flukes). The flippers are large. The length of the rostrum is less than double the length of the cerebral section of the skull. Teeth $\frac{35-44}{35-44}$. Vertebrae 79-81.

The body is well proportioned, resembling the common dolphin (Fig. 240). The forehead is low and long. The color is pale bluish-black



451 Fig. 240. Malay [Pan-tropical spotted] dolphin, *Stenella dubia* (figure by N.N. Kondakov).

above, ash-gray or grayish-white below. Numerous minute whitish or grayish, sometimes pinkish spots are scattered over the body. A dark band runs from the flippers to the corner of the mouth. The upper jaw and lateral sections of the lower jaw are black. The tip of the "beak" is white. A band runs forward from a black spot around the eye.

The main body measurements (as percentage of body length) of males with a body length of 165-208 cm and females 180-201 cm (Nishiwaki, 1966) are respectively: from end of upper jaw to blowhole 14.2-17.1 and 14.2-17.7, from fork between caudal flukes to posterior edge of dorsal fin 39.2-40.5 and 39.6-42.8, from caudal fork to anal opening 25.2-26.5 and 25.2-27.2; length of flippers 14.4-15.1 and 12.0-15.2, maximum width of flippers 5.0-5.3 and 4.2-5.3; length of base of dorsal fin 12.1-14.2 and 12.4-14.2, height of dorsal fin 8.2-9.7 and 7.8-9.4; and width of caudal flukes 21.6-22.5 and 23.5.

The main dimensions of the skull (as percentage of condylobasal length) of these dolphins with a condylobasal length of skull 381-428 mm (Nishiwaki, 1966) are: length of rostrum 58.5-61.5 and its width at the base 21.5-23.3; interorbital width 38.8-42.8; length of lower jaw sections 84.5-90.3, and length of symphysis of lower jaw 16.0-17.3. (V.S.)

The presence of this species in USSR waters has not been established. Presence in or transgressions into the waters of the Sea of Japan and around the Kuril Islands are possible.

Outside the USSR, this species is found in the South Atlantic Ocean up to Cape Horn and Cape of Good Hope, the Indian Ocean, the Pacific Ocean from New Zealand to the South China Sea, Hawaiian Islands, and waters of Japan. (V.H.)

Biology is not known.

BRIDLED [ATLANTIC SPOTTED] DOLPHIN⁵

Stenella frontalis G. Cuvier, 1829

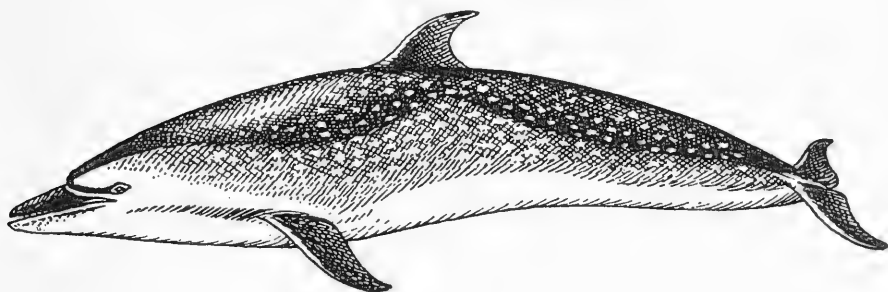
1829. *Delphinus frontalis*. G. Cuvier. Règne Animal, I, p. 228. Cape Verde Islands, Atlantic Ocean. (V.H.)

Body length about 180 cm. Color of the dorsal section blackish, changing over to grayish on the flanks. Abdomen whitish. The dorsum has light-colored and the abdomen dark spots. A dark-colored band runs from the corner of the mouth toward the flippers (Fig. 242). The eyes are encircled
452 by black rings. The flippers are small. The length of the rostrum is less

⁵ The Russian name is given here.



451 Fig. 241. Malay dolphin, *Stenella dubia*, seen from underside (figure by N.N. Kondakov).



452 Fig. 242. Bridled dolphin, *Stenella frontalis* (figure by N.N. Kondakov).

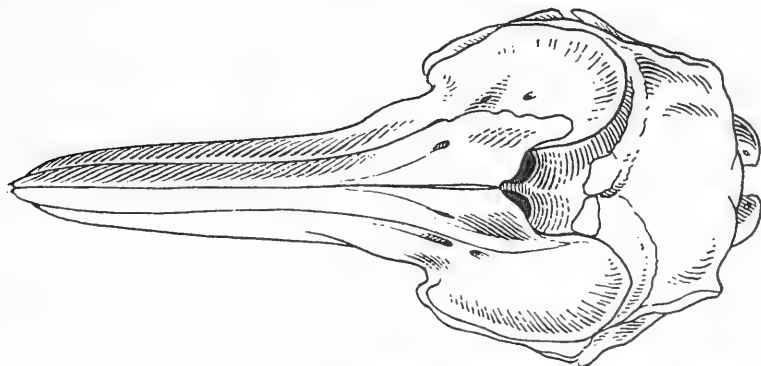
than double the length of the cerebral section of the skull (Fig. 243).

Teeth $\frac{35-44}{35-44}$ (usually $\frac{37-38}{37-38}$).

Vertebrae: 7 cervical, 15 thoracic, 19 lumbar, and 36 caudal; total 77. Phalangeal formula: I_{2-3} , II_9 , III_7 , IV_3 , and V_{2-} (V.S.)

Its residence has not been established in the waters of the USSR. Habitation in or transgressions into the Sea of Japan are possible.

Outside the USSR, it is found in the Atlantic Ocean (from Cape Verde Islands to Cape of Good Hope and from North Carolina to



453 Fig. 243. Skull of the bridled dolphin, *Stenella frontalis* (figure by N.N. Kondakov).

Florida), Mediterranean Sea, and Indian Ocean. It has been reported in the waters of Japan and the Korean peninsula (Cheju-do Island and Sea of China). (V.H.)

Biology is not known.

LONG-SNOUT [SPINNER] DOLPHIN

Stenella longirostris Gray, 1828

1828. *Delphinus longirostris*. Gray. Spicil. Zoologica, 1, p. 1. Type locality not established.

1846. *Delphinus alope*. Gray. Zoology, Voyage Erebus and Terror, 1, pl. 32.

1846. *Delphinus roseiventris*. Wagner. Schrebers Säuge thierte, 7, pl. 360. (V.H.)

Body length roughly up to 213 cm. Dorsal side of body dark gray. The abdomen is white with random gray spots. The flippers are small (Fig. 244). The length of the rostrum is double the length of the cerebral section of the skull (Fig. 245). The bony palate has very small longitudinal grooves. Teeth $\frac{45-56}{45-56}$ (usually $\frac{50-52}{50-52}$). Vertebrae 72-73. (V.S.)

Its residence has not been established in USSR waters. Habitation in or transgressions into the Sea of Japan are possible.

Outside the USSR (Fig. 246), it is reported in the Atlantic Ocean south of the Bahamas and Senegal up to Cape Horn and Cape of Good Hope, the Indian Ocean (Ceylon), and the Pacific Ocean from Mexico and Japan to Australia. (V.H.)

Biology is not known (Fig. 247).

Genus of Common Dolphins

Genus *Delphinus* Linnaeus, 1758

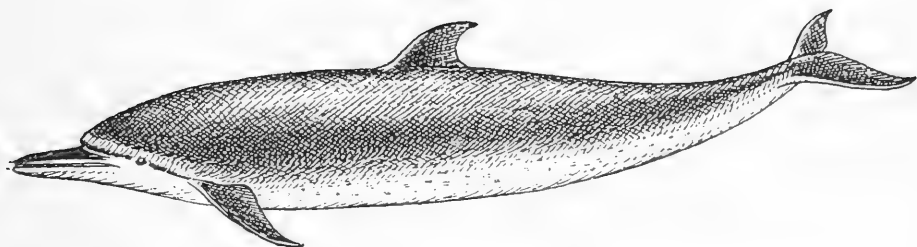
1758. *Delphinus*. Linnaeus. Syst. Nat., ed. X, 1, p. 77. *Delphinus delphis* Linnaeus, 1958.

Small cetaceans with body length up to 2.6 m.

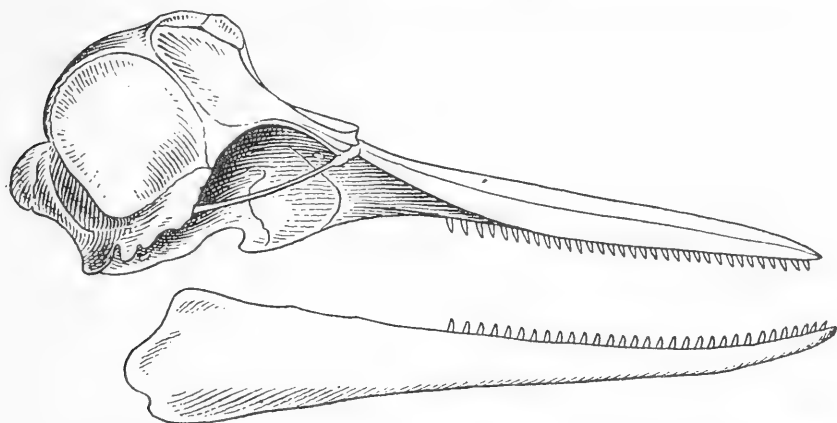
The "beak" is long. The dorsal fin is high and crescent-shaped. The narrow flippers are also curved.

Body coloration is subject to considerable individual variation but is usually black above, gray with dark- and light-colored bands on the flanks, and light-colored below.

455 The rostrum is 1.5 to 2 times longer than the cranium and bifurcated anteriorly. Two longitudinal grooves occur on the bony palate. The pterygoid bones are adjacent throughout their length. The supraoccipital



453 Fig. 244. Long-snout dolphin, *Stenella longirostris* (figure by N.N. Kondakov).



453 Fig. 245. Skull of the long-snout dolphin, *Stenella longirostris* (figure by N.N. Kondakov).

crest is asymmetric: its right half is larger than the left. The lower jaw is slightly longer than the upper. The teeth are conical and number $\frac{39-65}{39-64}$. Vertebrae 70-75. Phalangeal formula: I_{2-3} , II_{8-9} , III_{5-7} , IV_{2-4} , and V_{1-2} . The 2nd and 3rd digits are the longest. Ribs, up to 15 pairs. The sternum is complete and T-shaped.

These are pelagic forms living on fish. The females are capable of annual reproduction. Gestation extends for roughly 10 months and lactation for four months. The females may ovulate and can be fertilized during the lactation period.

These animals are distributed in all the oceans and most of the seas in the temperate and warm parts of the world.

The genus comprises a single species, the common dolphin, *D. delphis* Linnaeus, 1758. Some scientists (for example, Nishiwaki, 1972) recognize two more species: *D. capensis* Gray, 1828 and *D. bairdi* Dall, 1873.

These animals could be of economic importance. (V.S.)

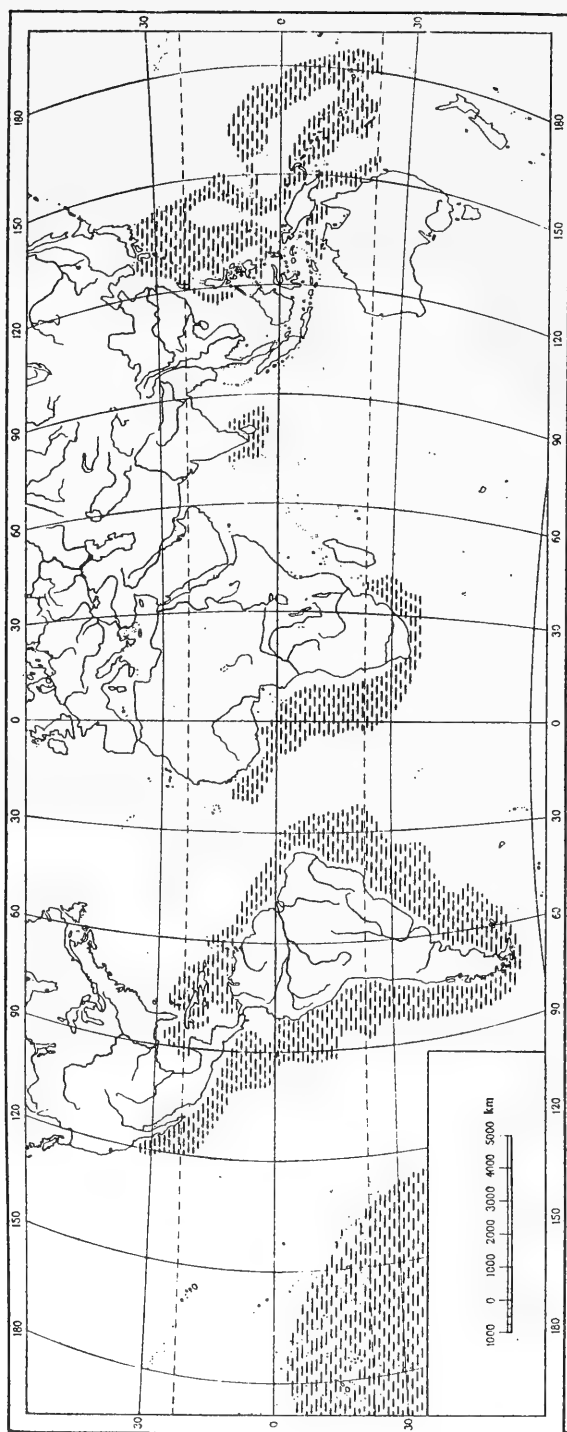
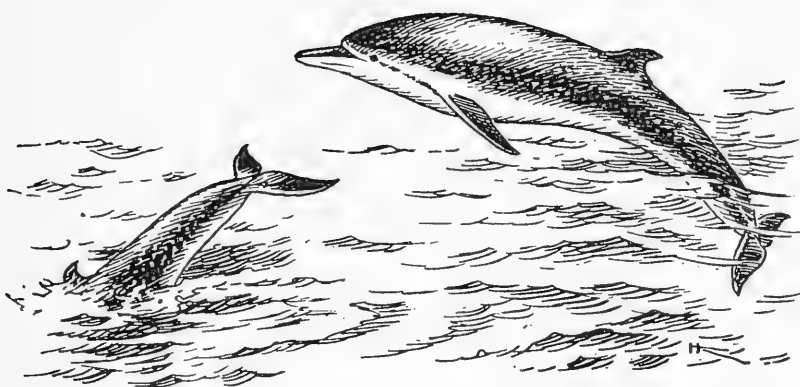


Fig. 246. Range of the long-snout dolphin, *Stenella longirostris* (V.A. Arsen'ev).



455 Fig. 247. Long-snout dolphin, *Stenella longirostris*, at sea (figure by N.N. Kondakov).

COMMON DOLPHIN

Delphinus delphis Linnaeus, 1758

1758. *Delphinus delphis*. Linnaeus. Syst. Nat., ed. X, I, p. 77. Waters of Europe ("Oceano Europeo").
1860. *Delphinus algeriensis*. Loche. Rev. Mag. Zool. Paris, 12, p. 474. Algeria.
1873. *Delphinus bairdii*. Dall. Proc. California Acad. Sc., 5, p. 12. Point Arguello, Santa Barbara, California.
1883. *Delphinus delphis* var. *curvirostris*. Riggio. Nat. Sicil., 2, p. 158. Mediterranean Sea.
1935. *Delphinus delphis ponticus*. Barabash-Nikiforov. Byull. Mosk. Obshch. Ispyt. Prirody, 44, p. 249. Yalta, Black Sea. (V.H.)

Diagnosis

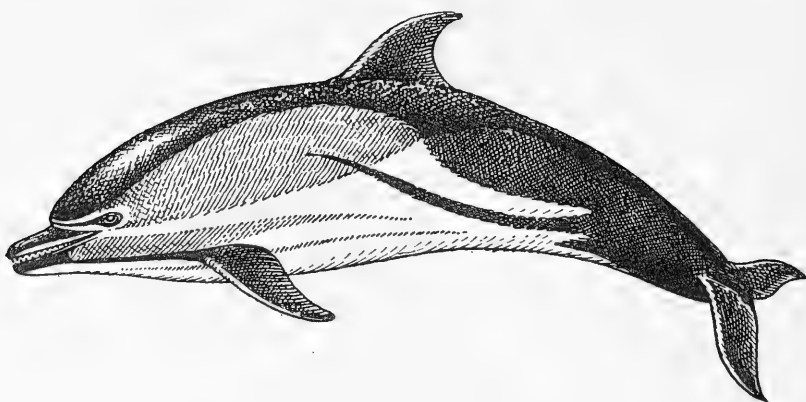
Single species of the genus.

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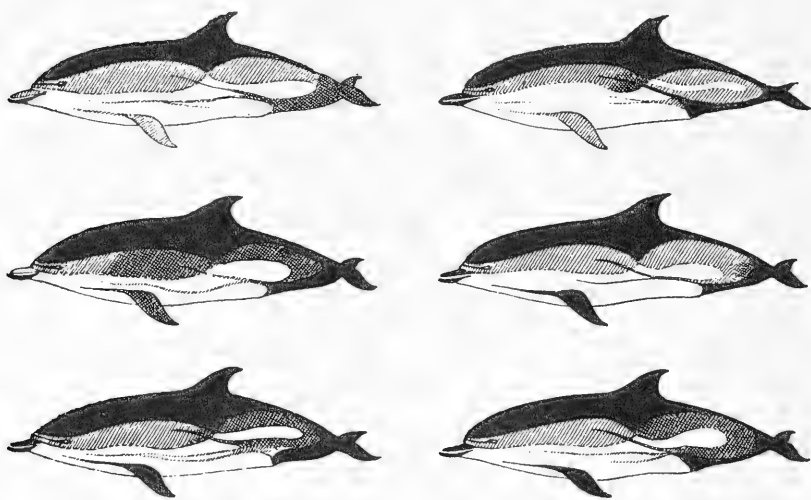
Description

Well-proportioned animals with a moderately elongated body, distinctly demarcated long beak, and relatively high dorsal fin (Fig. 248).

The body color is a combination of black and white and intermediate shades of the same. The upper part of the body is dark-colored and the underside is white; two gray elongated fields and one to three gray bands extend from the zone of the anal opening to the anterior half of the body along the flanks. One dark-colored band runs from the chin to each of



456

Fig. 248. Common dolphin, *Delphinus delphis* (figure by N.N. Kondakov).

457

Fig. 249. Variation in coloration of the common dolphin, *Delphinus delphis* (figure by N.N. Kondakov).

the flippers. A narrow dark-colored strip joins the eyes at the bridge of the nose. The flippers, caudal flukes, and dorsal fin are dark-colored. Color combinations of Black Sea dolphins vary markedly (Fig. 249). Far Eastern common dolphins are differentiated from their Black Sea and Atlantic counterparts by distinctly visible lateral and diagonal bands and by the fact that the dark color of the upper part of the body flanks is sharply demarcated from the light-colored underside (Tomilin, 1957).

In general, however, coloration is similar among animals from different parts of the range.

The skin cover has a thin dermal layer with loose fascicles of collagen fibers. At the boundary with the subcutaneous musculature, elastin fibers and even small fascicles are intertwined.

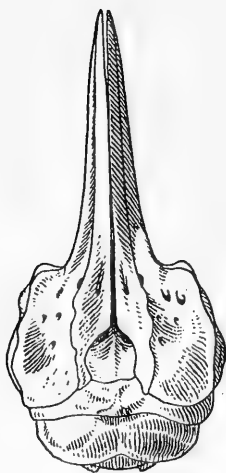
The usual number of vertebrae is: cervical 7, thoracic 14, lumbar 21, and caudal 31: total 73. Cervical vertebrae are often fused. Ribs 13-15 pairs; their number may differ on the left and right sides.

An instance has been reported of rudiments of the posterior limbs being detected along the flanks of the urogenital slit among some females caught in the Yalta region (Sleptsov, 1939). The rudiments are in the form of triangular lobes with a height of 3.4 cm (right) and 1.6 cm (left). Each contains two bony members (rudiments of femur and tibia), three cartilages on the right and two on the left (rudiments of tarsus, metatarsus, and phalangeal digits).

The main measurements (as percentage of body length) of adult male common dolphins (six) with a body length of 155 to 190 cm and young females (three) with a body length of 142 to 161 cm (Tomilin, 1957) are respectively: distance from tip of snout to anterior edge of dorsal fin 47.1 and 48.0, up to blowhole 17.9 and 19.6 (two measurements each), from anal opening to notch between caudal flukes 27.7 (three measurements) and 28.6 (two measurements), length of flippers, 16.3 and 17.0, maximum width of flippers 6.2 and 6.1, height of dorsal fin 10.3 and 10.1, length of dorsal fin along the base 15.9 and 14.3, and width of caudal flukes from fork to corner 11.8 and 12.3.

The most common body length of the Black Sea dolphin is 160-170 cm: males 161.8-165.8 cm and females 158-158.7 cm; maximum
457 length 210-219 cm. Dolphins with a body length exceeding 200 cm are extremely rare: of 38,000 or more dolphins examined, only 26 were longer than 200 cm (Barabash-Nikiforov, 1940). Atlantic and North Pacific common dolphins are larger than their Black Sea counterparts: the maximum body length of the former reaches 258 and 259 cm respectively.

Individual variation in skull dimensions (Fig. 250) is very significant (Kleinenberg, 1956a). The height and width of the occipital foramen, size of the parietotemporal fossa, length of the basilar bone [OCHObHbI KOCTb, basilar process], height of the rostrum, as also the number of teeth are highly variable. The total and base length of the skull and the height of the occipital region are relatively stable. Sexual dimorphism of the skull is poorly manifest (Tryuber, 1937). Among males, the skull length relative to body length is less, the cerebral section and rostrum shorter, while the frontal section on the contrary, is greater than among



457 Fig. 250. Skull of the common dolphin, *Delphinus delphis* (figure by N.N. Kondakov).

females. With the jaws closed, the rostral portion of the skull of males resembles a broad obtuse wedge while in females it is more pointed and elongated.

The main dimensions of the skull (as percentage of total length of skull) of 23 adult males with an average total skull length of 39 cm and 11 adult females with an average skull length of 38 cm (Black Sea; Kleinenberg, 1956a) are respectively: length of frontal section 72.3 and 71.7, cerebral section 27.7 and 28.3, height of occipital region 31.6 and 31.2, width of cranium 35.7 and 35.5, length of rostrum 60.2 and 60.2, width of rostrum at the base 21.0 and 20.6, height of rostrum at the last tooth 8.0 and 7.7, and length of lower jaw 84.7 and 84.7.

458 Age-related changes in the skull (Tryuber, 1937; Barabash-Nikiforov, 1940; Tomilin, 1957) are significant. In the newborn, the cranium does not have crests, the skull bones are not completely fused, and the teeth have not cut through. In the first year, sutures between the bones are closed, crests are formed, and the teeth cut through (45-48 in each jaw). On taking to independent feeding, the muscular apparatus strengthens due to the greater dimensions of the crests and projections and the rotundity of the skull disappears. Skull growth is most vigorous in the first two years; increase in total length of the skull mainly occurs in the frontal section. At this time the dental system is fully developed. By three years of age, the skull is finally formed. Crests in the skull attain maximum development by four to five years of age. (V.S.)

Geographic Distribution

These animals inhabit the temperate and warm waters of the Atlantic, Indian, and Pacific oceans in both the hemispheres.

Geographic Range in the USSR

Black Sea, Sea of Japan, Sea of Okhotsk, Pacific Ocean around the Kuril Islands, Bering Sea, waters of southern Kamchatka, and Commander Islands (Fig. 251).

These dolphins may be present in our waters of the Baltic Sea since they transgress (albeit rarely) into the southern part of the sea and even up to the estuary of the Visla (Koval'skii, 1964). Transgression into the Barents Sea is also possible.

Geographic Range outside the USSR

In the North Atlantic, it reaches the coasts of northern Norway, Iceland, the southern coasts of Greenland, and is encountered in Newfoundland and the Gulf of St. Lawrence (Fig. 252). It is quite common in the Mediterranean Sea and is encountered on the Canary Islands and along the entire African coast right up to the Cape of Good Hope and Tristan da Cunha Island. In the western part of the Atlantic, it is known in the
 460 Bahamas, the Gulf of Mexico, the Caribbean Sea, and in the waters of South America up to 45° S lat. It inhabits the entire Indian Ocean and is known in the south along the coasts of Tasmania and Australia. In the Pacific Ocean, it inhabits from Kamchatka and British Columbia south to the Australian and New Zealand coasts and along the coasts of Chile up to 45° S lat. (V.A.)

Geographic Variation

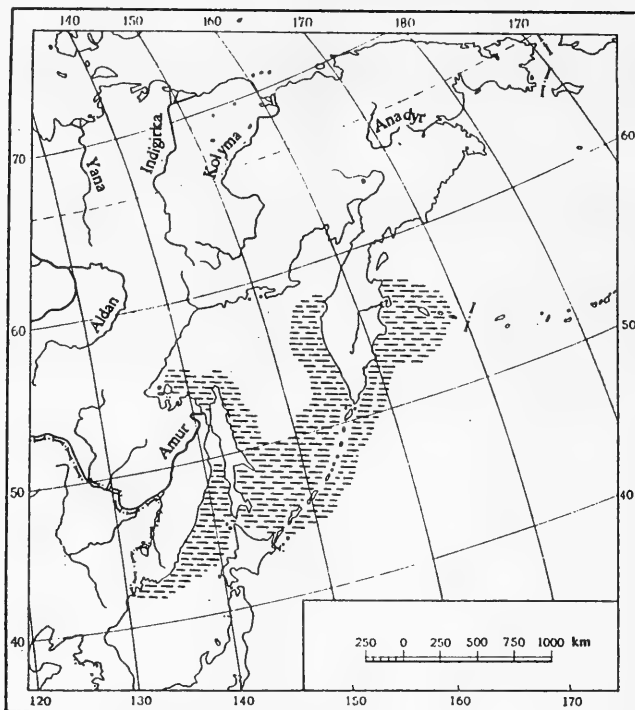
This aspect has not been adequately studied. Based on the main dimensions and coloration of the animals, a few subspecies have been described. Of these, three inhabit or transgress into the waters of the Soviet Union.

1. **Atlantic common dolphin**, *D. d. delphis* Linnaeus, 1758.

Largest of the forms, with an average body length of adults at 225 cm. Color variation is very significant.

Its presence in the Barents and Baltic seas is possible.

Outside the USSR, it is found in the waters of the Atlantic Ocean in the Northern as well as Southern hemisphere.



458 Fig. 251. Range of the common dolphin, *Delphinus delphis*, in the Pacific Ocean waters of the USSR (V.A. Arsen'ev).

2. Black Sea common dolphin, *D. d. ponticus* Barabasch, 1935.

Smallest in skull and body dimensions; body length of adults averages 204 cm.

Color variation relatively minor.

Black Sea.

Outside the USSR, it is found in the waters of Turkey, Bulgaria, and Rumania.⁶

3. Pacific common dolphin, *D. d. bairdi* Dall, 1873.

In body dimensions it occupies an intermediate position between the two preceding forms. The average body length of adults is 208 cm; thus it is larger than the Black Sea but smaller than the Atlantic form.

Waters of the Pacific Ocean.

⁶ The characteristics of the Black Sea and Atlantic common dolphins have been analyzed and compared. However, no comparison with the Mediterranean populations has been done, which is essential. (V. H.)

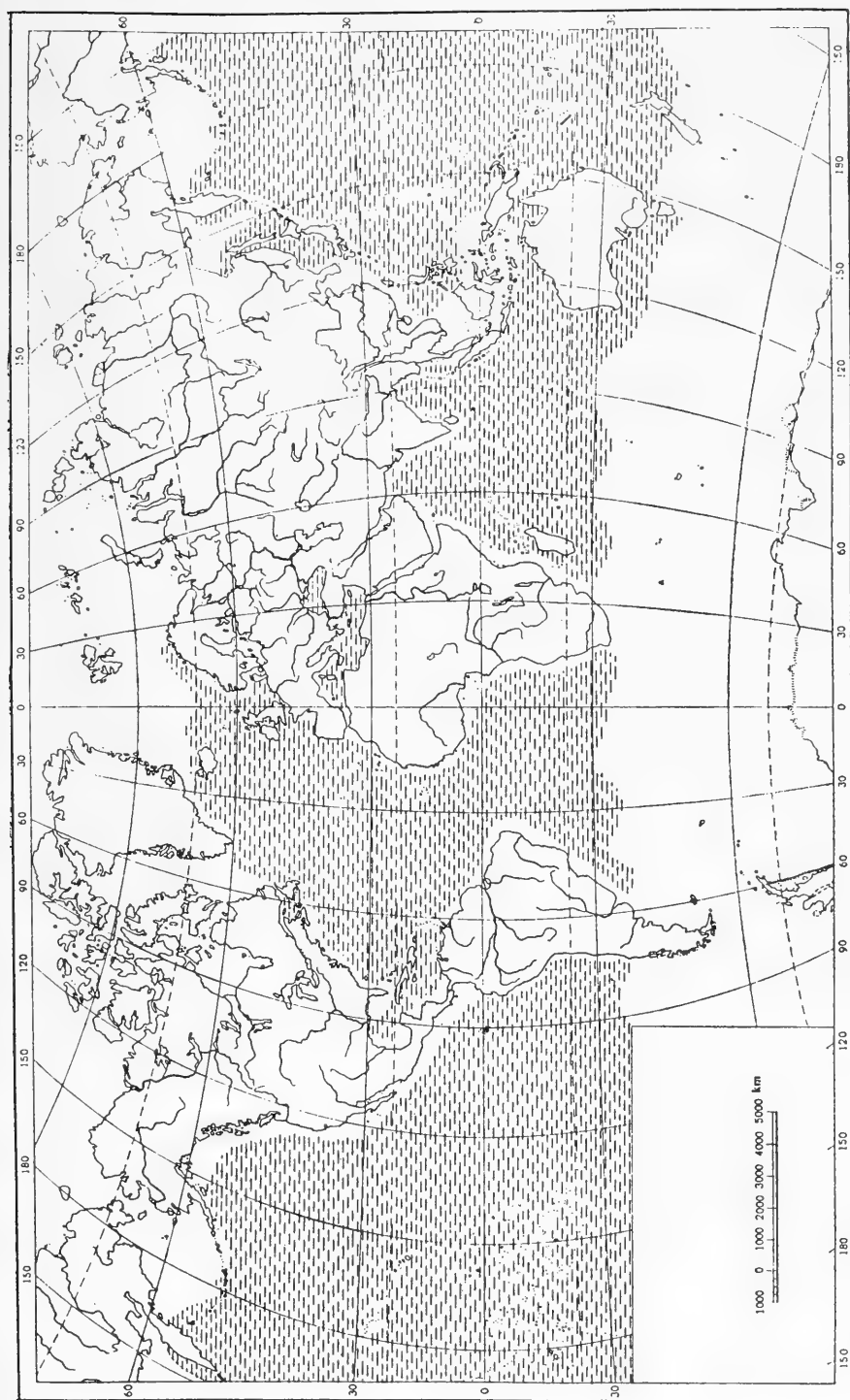


Fig. 252. Range of the common dolphin, *Delphinus delphis* (V.A. Arsen'ev).

Outside the USSR, it is found throughout the North Pacific Ocean. (V.A.)

Biology

Population. The total population of the Atlantic and Pacific subspecies has not been established. The population of the Black Sea common dolphin, in spite of the fact that this subspecies inhabits a comparatively small landlocked water body, apparently reached 1.5 to 2 million, with the catch in some years in the Black Sea exceeding 100,000. At present, however, its population is considerably reduced, and probably does not exceed 200,000 to 250,000 animals.

Food. The food of the Black Sea common dolphin is fish, crustaceans, and mollusks. The common dolphin feeds on anchovy (*Engraulis encrasicolus*), pelagic pipefish of the family Syngnathidae (evidently, *Syngnathus schmidtii* and *Sighonostomus typhle*), sprat (*Sprotella sprotus phalaerica*), haddock (*Gadus euxinus*), scad (*Trachurus trachurus*), mullet (*Mullus barbatus*), and bluefish (*Tomnodon saltator*) [*Pomatomus saltatrix*]. From among crustaceans, large isopods (*Idothea algerica*) and the shrimp (*Crangon crangon*) (sometimes stray specimens) form the food of this subspecies; from among mollusks, *Nassa reticulata*, *Macra subtruncata*, *Guoldia minima*, *Venus gallina*, *Colyptera hinensis*, *Modiola adriatica*, *Mytilaster* sp., and *Fellina fabula*, constitute the food of this subspecies.

Three types of fish form the food base. These are anchovy, pelagic pipefish, and sprat, i.e., small schooling fish often forming large concentrations. All of the other species are rarely encountered and, in small numbers, in the stomach of this dolphin, constituting a few tenths of a percent of the total food. Dolphins swallow mollusks incidentally during the intake of fish, mainly anchovy.

The food of the Black Sea dolphin changes, depending on the region of habitation and the season of the year (Table 35). In winter and early spring months, in the coastal zone, dolphins feed exclusively (or almost so) on anchovy. In summer and autumn, pelagic pipefish predominate in terms of frequency of encounter but are of minor significance in the entire food. Sprat in this respect plays a major role, although in terms of frequency of encounter, it is slightly inferior to the pelagic pipefish (Kleinenberg, 1940).

In the summer months, the common dolphin forms massive schools in the open sea and the food composition there differs sharply from that established for the coastal zone (Table 36).

In the coastal zone, this dolphin feeds on many species of fish but almost exclusively on sprat in the open sea. However, from May through

Table 35. Food of the common dolphin in the coastal zone of the Black Sea, % (Kleinenberg, 1956a)

Region	January		February		March		April		May		June	
	Food item	%	Food item	%	Food item	%	Food item	%	Food item	%	Food item	%
Batumi	Anchovy	100	Anchovy	100	Anchovy	100	Anchovy	98	—	—	—	—
							<i>Idothea</i>	2				
Novyi Afon	Anchovy	100	Anchovy	98	Anchovy	100		—	—	—		
			<i>Idothea</i>	2								
Novorossiisk	Anchovy	78	Anchovy	50	Anchovy	40	Anchovy	38	—	—	Pelagic pipefish	98
	Sprat	22	Sprat	25	Sprat	12	Sprat	1	—	—	Anchovy	2
			Pelagic pipefish	25	Pelagic pipefish	44	Pelagic pipefish	59	—	—		
					<i>Idothea</i>	2	<i>Idothea</i>	1				
			Haddock		Haddock	2	Haddock	1				
Yalta	—	—	—	—	Anchovy	100	Anchovy	100			Pelagic pipefish	70
											Anchovy	8
											Sprat	13
											<i>Idothea</i>	4
											Haddock	3
											Bluefish	2

(contd.)

Table 35 contd.

	July		August		September		October	
	Food Item	%	Food item	%	Food item	%	Food item	%
Novorossiisk	Pelagic pipefish	38	Pelagic pipefish	86	Pelagic pipefish	85	Pelagic pipefish	45
	Anchovy	32	Anchovy	7	Anchovy	13	Anchovy	44
	Sprat	26	Scad	4	Haddock	1	Sprat	10
	Scad	3	Bluefish	3	Bluefish	1	Haddock	1
	Haddock	1						
Yalta	Pelagic pipefish	37	Pelagic pipefish	57	Pelagic pipefish	90	Pelagic pipefish	85
	Anchovy	32	Anchovy	32	Sprat	9	<i>Idothea</i>	1
	Sprat	12	Sprat	6	<i>Idothea</i>	1	Haddock	8
	<i>Idothea</i>	9	<i>Idothea</i>	3			Mullet	6
	Haddock	9	Haddock	2				
	Bluefish	1						

462 Table 36. Food of the common dolphin in the coastal zone of northern Caucasus and away from coasts (Tsalkin, 1938a)

	Percentage of total number of items detected	
	In coastal zone (S.E. Kleinenberg)	Away from coasts
Pelagic pipefish	72.0	—
Anchovy	15.0	0.1
Sprat	—	99.6
Haddock	1.0	0.3
<i>Idothea</i> (slater)	1.5	—
Scad	8.0	—
Mullet	—	—
Bluefish	2.0	—

August, sprat serves as the main food not only in the open sea, but also in the coastal zone, constituting, on average, over 90% of the food for the season as a whole. In various regions, the age composition of sprat varies sharply in different months. In May, the stomach of the dolphins in the coastal zone as well as in the open sea contained both adult and young sprat, while in June in the open sea, the preference was for young sprat and in the coastal zone of Crimea (Alushta) and the Caucasus (Gelendzhik), mainly the adult fish. In July and August, the stomach of all the dolphins from all the regions contained mainly young sprat. Thus young sprat constituted the maximum specific proportion in the food of these dolphins in the summer months (Tarasevich, 1958b).

The seasonal change in the food of the Black Sea common dolphin is explained by the biological features of the fish consumed by it. Sprat is a cryophilic fish and its spawning continues throughout the winter and spring months. In the period of spawning, sprat is scattered over immense pelagic regions of the sea and does not form significant concentrations. In summer, however, young sprat as well as adult fish remain sufficiently concentrated and hence serve as the main food of these dolphins at this time. Anchovy, on the other hand, is a thermophilic fish and spawns in the summer months. At this time it is also scattered over a large expanse in the coastal zone as well as in the open sea and nowhere forms noticeable concentrations. In the winter months, anchovy gathers at certain places, i.e., in regions of steep precipitous drops of coastal waters. In December, massive collections of anchovy form almost simultaneously along the southern coasts of Crimea (Balaklava-Sarych region) and the Caucasus (Poti-Batumi region). It is in this period that anchovy serves as the main food of these dolphins (Freiman, 1950).

Thus the main food items of the common dolphin lead a pelagic way of life, are relatively small in size, and form dense concentrations.

Information on the food of Atlantic and Pacific subspecies of the common dolphin is very scant. Fish apparently serve as their main sustenance. Sardines, flying fish, anchovy, herring, mackerel, and gray mullets have been indicated as food items. Sometimes crustaceans and mollusks (bivalves and cephalopods) are encountered. In a dolphin caught close to Corsica, the stomach contained four specimens of *Enoploteuthis margaritifera* and three of *Chirteuthis veranyi* in addition to *Loligo vulgaris*, *Todarodes sagittatus*, *Onychoteuthis lichtensteini*, *Heteroteuthis dispar* (?), and three squids identified as *Ctenopteryx cyprinoides* (Tomilin, 1957). The stomach of a dolphin caught on May 22, 1957 in Newfoundland contained the remains of 20 Atlantic shortfin squids, *Illex illecebrosus*, which are quite numerous in these waters in summer (Sergeant, 1959b).

Daily activity and behavior. No changes have been observed in the daily activity of dolphins. Fast and impetuous movements are characteristic of the common dolphin, as in the case of many other species.

463 Feeding mainly on pelagic fish, the common dolphin does not go very deep and short respiratory intervals are characteristic. It usually emerges onto the water surface every 0.5 - 1 min, less often every 1.5 - 3 min. It can remain submerged in water for a maximum of 5 min. The duration on the surface is reckoned at a few tenths of a second. The common dolphin does not produce blows and splashes water sideways only slightly.

Foraging dolphins move slowly and submerge steeply in the water. When feeding on fish schools confined roughly at one place, the dolphins dive almost vertically. They cannot perhaps dive deeper than 70 m since they never descend below the lower seine ropes of 70-m high fishing nets.

A "traveling" dolphin swims rapidly, easily overtaking ships sailing at 15-18 miles an hour. It swims right on the surface of the water and at short intervals (at the time of inhalation/exhalation) leaps powerfully out of the water, often over a span of up to 10 m (Fig. 253). The habit of dolphins running behind ships is interesting. Small schools very often accompany a ship for a few hours, sometimes on one side, sometimes on the other, straying off and again rapidly closing in. Dolphins usually love to play before the very stem, leaping out of the water into the surf formed by the ship. When moving in schools, the dolphins do not leap simultaneously; thus at any given moment a few animals can be seen on the surface of the sea (Kleinenberg, 1956a).

The females are greatly attached to their calves. Two females swam for a long time around a sweep net enclosing a water body in which their calves were held.



Fig. 253. Leaping common dolphins (photograph by S.E. Kleinenberg).

The auditory faculty is well developed among dolphins. Common dolphins are frightened of sharp sounds, which in fact is taken advantage of when trapping them in sweep nets. A school of dolphins is chased away from the wall of the net using a "telephone", i.e., striking stones one against the other in the water (Tomilin, 1957). Vision is not as well developed as hearing. Dolphins can probably see in water no more than a few tens of meters. They produce extremely diverse sounds—whistling, squeaking, and crackling. Some sounds are produced at high frequencies, beyond the range of human perception. Such sounds are used by the dolphin for echolocation, enabling excellent self-orientation in an aquatic environment.

The age and sex composition of schools of dolphins vary at different times of the year. In winter, two types of schools have been noticed. The first type, called the winter female groups, consists of 40 to 50% mature females, some gestating, some barren, and those that have only recently attained maturity (lactating females are very few) and 50 to 60% immature animals of both sexes. Immature females in these schools represent all age groups while immature males are usually young. Much larger males, approaching maturity, are found in small numbers. Schools of the second type are called male groups and contain predominantly males, to the extent of 90% of the total number of animals in a group in January-February and about 80% in March-April. The females in these schools, at best, account for 10-20% and comprise mainly the barren with only 4-5% being immature. Most of the males in the school are

mature animals while the immature are mainly represented by older age groups.

The following types of schools have been established for the spring-summer months: with the approach of the en masse calving season (March-April), the gestating females begin to separate from the female schools and gradually form individual precalving schools.

The maximum number of such schools is formed in May and June but the precalving schools invariably contain immature animals too, which sometimes constitute up to 30% and even 45% of the school's strength. As the gestating females leave the winter female schools, the remaining dolphins form independent groups. In some cases, they consist of mainly the immature animals of both sexes and may be called schools of immature dolphins. Such schools formed in March represent long-time formations and are seen later throughout the year. If, however, the winter female schools comprise mainly young and barren females, with only a few gestating ones, after the separation of the latter, residual female groups are formed with predominantly barren and just recently matured females. These groups remain active for a short duration, i.e., only in early spring.

Females of the Black Sea common dolphin in the period preceding calving concentrate in regions with more favorable meteorological conditions, in the so-called calm zone. The animals find such conditions in the open sea far away from the coasts. It is here that precalving groups remain and are gradually transformed into schools of calves. The period of parturition is very prolonged in this dolphin and hence the number of gestating females in the precalving groups diminishes gradually while the number of lactating females concomitantly increases. Later, the lactating females begin to predominate and such groups can be called nurseries. Nevertheless, they invariably contain immature dolphins too and their relative proportion is even slightly more than in the precalving groups. Schools of calves are encountered mainly in the second half of June and in July. In August, and more so in September, they become quite rare.

Females begin to gather with the winter male schools in spring and by April-May such groups are transformed into breeding schools consisting of 60-80% mature males and females in roughly an equal proportion. Such groups are most often seen in the period of en masse mating (in July and August) and hence are called breeding schools. In the early spring months, they are formed by the merger of male and female groups (as soon as the gestating females have left the latter). Therefore, at this time the breeding schools contain only barren and recently matured females. In the summer months, lactating females join them in large numbers

and in July and August, form the bulk of the females in the school. The
465 growing juveniles form the majority of immature animals present in the
breeding schools.

The process of reformation of summer into autumn schools and the order of formation of winter types of common dolphin schools of the Black Sea population has not been traced (Tarasevich, 1951).

The above extremely schematic description reflects the process of formation of schools of different types and their transformation from one type into another. In nature, this process is far more complex. Such a diversity of schools and the numerous transformations which they undergo in the course of a year with respect to age and sex composition, compel us to estimate very carefully the percentage ratio of different age and sex groups in a school of dolphins using the data of hunters. Not only the time, but also the region of catch should be taken into consideration.

The common dolphin has been observed amidst groups of other species of dolphins, such as the bottlenose dolphin, the shorthead dolphin, and even the pilot whale. The common dolphin does not take very kindly to captivity compared to the other species and usually does not survive for more than two or three months in ocean aquariums. Its reproduction in captivity is not known (Tomilin, 1962).

Seasonal migrations and transgressions. The nature of seasonal migrations among Atlantic and Pacific subspecies has not been established. This aspect has been studied somewhat better for the Black Sea subspecies and it has been assumed that the common dolphin in general does not perform seasonal migrations; instead its movements should be regarded as migrations in search of food (Tomilin, 1957). These assumptions give rise to serious doubts, however.

The common dolphin is a typical pelagic animal avoiding sections with fresh and turbid waters and evidently, therefore, does not enter the Azov Sea (Freiman, 1950). It does not dive very deep in search of food but is satisfied with what is available in the upper horizons of the sea. It inhabits almost the whole of the Black Sea, in the coastal zone of Crimea, the Caucasus, Turkey, Bulgaria, and Rumania and also far away from the coasts. But its distribution in the equatorial seas is very uneven.

In winter months, in the period of spawning, sprat is scattered over a large water body and is almost not utilized as food by this dolphin. At this time the Black Sea anchovy concentrations are formed at the wintering sites in the coastal waters of Georgia (Poti-Batumi) and on the southern coast of Crimea (Balaklava). The presence of anchovy determines the wintering regions of the common dolphin, most of which concentrate on the coasts of Georgia and a small percentage south of the Crimean

peninsula. In spring, as the water begins to warm up, anchovy begin to spawn and are scattered over a large expanse without forming concentrations. Simultaneously, adult sprat and their young begin to concentrate in the coastal waters of Crimea and northern Caucasus and in the open northeastern waters of the Black Sea. Dolphins in search of food at this time move northwest where they encounter sufficient collections of sprat on which they feed in summer.

Depending on the collections of food objects, the common dolphin forms concentrations of different types: (1) encountered very rarely—only a few animals or small schools separated from each other; (2) encountered rarely—some animals live everywhere while schools are small and sparse; (3) encountered very frequently—numerous small- and medium-size schools (up to 100 animals each) predominate, large schools are very rarely seen; (4) encountered very often—large number of predominantly large schools, of the order of hundreds or thousands of animals in each, forming dense congregations in an extremely small water body (Tsalkin, 1938). These dolphins usually form congregations in the Tuapse-Sochi region along the coasts of the Caucasus; they may be closer or farther away from the coasts (20 to 60 miles) in different years. These are not long-time schools, surviving for just one to three
466 months. Simultaneous with them, schools of different strengths and some individual dolphins are very widely distributed along the Black Sea in the coastal zone as well as in the open sea, depending on the availability of food. In some years, the distribution of the groups and much smaller formations changes considerably according to seasonal conditions (Tarasevich, 1958a).

As the dispersal of sprat concentrations increases, schools of dolphins begin to abandon the regions of summer habitation and gradually gather at the wintering sites where they live throughout the winter months. The migrations of the Black Sea common dolphin are very small but they bear a distinctly manifest seasonal character and are quite constant in time and direction. There is every reason to consider them seasonal migrations, therefore, at least in the eastern part of the Black Sea. The periods and nature of migrations of the common dolphin in the western part of the sea have yet to be established.

In the Bay of Bosphorus, schools of dolphins swimming in different directions are often noticed. It is possible that the common dolphin sometimes leaves the Black Sea for the Sea of Marmara or, contrarily, transgresses from the Sea of Marmara into the Black Sea, but there is no recorded proof of this (Freiman, 1950). It has been assumed that a more intense exchange prevails between the Black Sea and the Mediterranean

Sea dolphins than is usually acknowledged, which might be reflected to some extent in the population dynamics of the dolphins of the Black Sea.

Reproduction. Mating and calving in the common dolphin are highly prolonged but there is no one single view on their duration. Various sources indicate that mating extends from June through October (Sleptsov, 1941), from July to December (Tomilin, 1957), and even from August to January (Maiorova and Danilevskii, 1934). But assumably most of these dolphins mate over a much shorter duration—in July, August, and the first half of September (Sleptsov, 1941); from August to October with peak activity in September (Tomilin, 1957); or in July (Kleinenberg, 1956a).

The period of calving, according to various authors, extends from May through November, peaking in June and July (Sleptsov, 1941); from May to October or from June to November, the majority of females calve from June to August, with maximum reached in July (Tomilin, 1957); or from May through September with the peak in May and June (Kleinenberg, 1956a). In any case, in most females parturition takes place in the summer months. Mating of the common dolphin has been observed time and again from airplanes and hunting craft. A group of mating dolphins consists of one female and six to eight males which pursue her at high speed, chase each other, and hold the competitor behind the fins with the teeth. When the fastest male catches up with the female, she turns her abdomen upward, mates with him, and the two then disappear into the water (Golenchenko, 1949b).

The duration of gestation has also been variously determined: about 10 months (Tomilin, 1957), 10-11 months (Kleinenberg, 1956a), and 11 months (Sleptsov, 1941).

The question of the periodicity of calving, i.e., the rate of replenishment of the population, has not yet been conclusively established. It was first thought that dolphins produced calves once every four years or twice in three years (Mal'm, 1936). According to M.M. Sleptsov (1941), dolphins tend to calve annually but since fertilization can occur only 1.5 to 2 months after birth, mating advances in time every year and the female becomes ready for fertilization afresh only after the males cease to mate. From this, it may be assumed that the female dolphins calve three years in a row but remain barren in the fourth. If this is so, then one out of four of the eligible females should remain barren every year (Kleinenberg, 1956a). According to V.E. Sokolov (1954), a calved female becomes capable of mating again within three to five weeks after parturition, i.e., even in the period of lactation, which would indicate the absence of advancement in the period of mating in subsequent years. Thus this dolphin usually reproduces every year and the percentage of

467 barren females in a group is not high (V.E. Sokolov, 1954). On this basis, it has been assumed that the sex cycle of the dolphin fits in the annual cycle, with a gestation period of 10 months (Tomilin, 1957). More reliable data are required before the question of the reproduction cycle of the Black Sea common dolphin can be conclusively resolved.

Growth and development. The uterine horns and ovaries are usually asymmetrical in the common dolphin; in 82.3% of cases, the left horn was wider and longer than the right one while the left ovary was larger; in 17.7% of cases, the right horn and the right ovary were larger. Probably, in an overwhelming majority of cases, the embryo (Fig. 254) grows in the left uterine horn (Sleptsov, 1941).

The newborn calf of the common dolphin reaches, on average, half the body length of the mother (sometimes more), which apparently is far more than the corresponding dimensions of newborns among other whales. The average body length of the newborn is 82-90 cm (Kleinenberg, 1956a). As a rule, one calf is born and twins are rare. The calf is born not head first, as thought earlier, but tail first. The dorsal fin of the embryo is convoluted and compactly pressed to the body and the caudal flukes are balled into a "fist" (Kleinenberg, 1956a).

Lactation extends for about four months (Tomilin, 1957) or five to six months (Sleptsov, 1941; Kleinenberg, 1956a). At the end of lactation, the stomach of calves contained fish remains along with milk. Milk production in the mammary glands of females is very little; thus a 168-cm long female could yield only 100 ml (Tomilin, 1957). Apparently the calf feeds often but in small portions. The composition of the milk of the common dolphin is shown in Table 37.



Fig. 254. Embryo of the common dolphin (figure by N.N. Kondakov).

Table 37. Chemical composition of the milk of the Black Sea common dolphin (Ural'skaya, 1957)

Composition of milk, %							Author and year of analysis
Fat	Protein	Sugar	Dry matter	Ash	Water	Total	
43.71	5.62	1.45	7.53	0.45	48.76	100	Mal'm, 1932
41.56	4.8	1.49	6.82	0.45	51.62	100	Ural'skaya, 1954

The growth of the common dolphin in different age groups has not been studied well. By autumn, the calf reaches a length of 100-110 cm, i.e., in the period of lactation, it adds 20-30 cm. With cessation of feeding on mother's milk (winter), growth slows down and by the next summer (toward the end of the first year) the dolphins reach a length of 120-130 cm. The average dimensions of two-year-olds is 140-150 cm and three-year-olds 165-170 cm. The length of most adult dolphins varies around 170 cm and their average weight 50-55 kg. Sometimes animals up to 200 cm long and 100 kg weight are encountered (Freiman, 1950). The common dolphin is characterized by sexual dimorphism: males are slightly larger than females right from the embryonic stage.

There is no unanimity of opinion regarding the time required to attain sexual maturity. According to some data, female common dolphins attain maturity in the third year and males in the fourth year (Sleptsov, 1941). According to other authors, females become mature at the end of the third year and males in the third or the fourth year (Kleinenberg, 1956a). According to still others, the common dolphin is capable of mating for the first time in the second year of life (Tomilin, 1957). The body length of these dolphins at the time of attaining maturity varies considerably. Mature females 140-150 cm long are encountered while some 161-170 cm long are still immature (Kleinenberg, 1956a). With a high degree of probability, it may be said that females with a body length of less than 155 cm should be regarded as immature and those longer than 155 cm as mature. This limit for males is put at a body length of 165 cm.

The maximum longevity of the common dolphin has been roughly put at 20-25 years (Sleptsov, 1941; Freiman, 1950).

Enemies, diseases, mortality, parasites, and competitors. The Black Sea common dolphin has no enemies. Subspecies of the Atlantic and Pacific oceans may become prey to the killer whale. There has been almost no study of the diseases afflicting this dolphin. Some instances of stones in the ureter (Kleinenberg, 1956a) and of skeletal diseases (Tomilin, 1957)

are known. From among skin parasites, crustaceans (*Xenobalanus globicitis*, *Penella pustulosa*, and *Larnaeonema nodicornis*) have been found.

Nineteen species of endoparasites are known: these include trematodes (six), cestodes (three), nematodes (six), and acanthocephalans (four). The trematode *Brauniina cordiformis* Wolf, 1903 is a parasite of the stomach and intestine of the common dolphin, the bottlenose dolphin and some species of spotted dolphins. Three species of trematodes of the genus *Campula* have been found in the bile duct and hepatic ducts of just the common dolphin: *C. delphini* Peirier, in individuals from the European waters of the Atlantic; *C. palliata* Looss, in the Atlantic subspecies (Europe) and Black Sea residents; and *C. rochebruni* Peirier, in specimens from the Atlantic waters of Europe. The trematode *Distomum philocholum* Creplin, which localizes in the liver, was detected in the common dolphin from European waters. The trematode *Galactosomum erinaceum* Peirier was found in the intestine of the common dolphin also only from European waters.

The cestode *Tetrabothrium fosteri* is a parasite of the intestine of the common dolphin and beaked whales. It has been found in the Mediterranean Sea and in the southern part of the Pacific Ocean. *Monorygma grimaldii* Monier localizes in the abdominal cavity, mesentery, and diaphragm of the common dolphin and four other species of dolphins of the Mediterranean Sea and the Atlantic Ocean. The cestode *Phyllobothrium delphini* Bosc is quite extensively distributed among marine mammals. In addition to the common dolphin, it has been detected in six species of toothed whales, the bowhead whale, and Weddell's seal. It localizes in the skin and hypodermic tissue and has been reported from the Atlantic Ocean, Mediterranean Sea, northern and southern parts of the Pacific Ocean, and in the Antarctic.

One of the most widely distributed species of nematode parasites, *Anisakis (Anisakis) simplex* Rudolphi, infects the gullet, stomach, and intestine. Apart from the common dolphin, it has also been detected in ten species of toothed whales, two species of baleen whales, and in Steller's sea lion. It has been reported in the North Sea and in different parts of the Pacific Ocean (Kamchatka, Japan, and New Zealand). Among the common and three other species of dolphins, *Anisakis (Anisakis) typica* Diesing is a parasite of the stomach while *Anisakis dussmeerii* Beneden has been found in the stomach and large intestine
 469 of only the common dolphin. The nematode *Halocercus (Halocercus) delphini* Baylis and Daubney was detected in the bronchi of the common dolphin only from the Atlantic Ocean while another representative of this genus, *Halocercus (Posthalocercus) kleinenbergi* Delamure, was found in the lungs of only the Black Sea common dolphin. Yet another species

of nematode, *Skrjabinalius cryptocephalus* Delamure, was found in the lungs of only the Black Sea common dolphin.

Of the four species of acanthocephalans, *Bolbosoma vasculosum* Rudolphi is a parasite of the intestine of common dolphins and beaked whales from the Mediterranean Sea and the Atlantic Ocean. *Bolbosoma bellicidum* Leuckart has been reported in the common dolphin. *Corynosoma cetaceum* Johnston, a parasite of the intestine of common and bottlenose dolphins, was detected in Australian waters. The specific affinity of the fourth representative of acanthocephalans, *Corynosoma* sp., has not been established (Delamure, 1955; Tomilin, 1962).

Natural mortality has not been studied. It appears possible that the common dolphin could die from an invasion of the nematode *Skrjabinalius cryptocephalus*, which has infected the lungs of some animals to such a degree that they were totally damaged (Kleinenberg, 1956a).

There are almost no competitors of the Black Sea common dolphin. The Atlantic and Pacific subspecies may be food competitors of other species of dolphins.

Population dynamics. In the prewar years, when the total catch of the common dolphin in the Black Sea sometimes exceeded 100,000 animals per year, a distinct reduction in population was noticed. During the years of the Great Patriotic War [WW II], hunting activity perforce declined and the population recouped slightly. Subsequently hunting resumed and the population decimation was such that hunting these dolphins was banned. Information on the population of the common dolphin in other parts of its range is not available.

Field characteristics. This is a rather small (body length of adults 150-170 cm) agile dolphin having a high pointed dorsal fin with a crescent-shaped notch in the posterior margin [falcate]. The beak is long and sharply demarcated from the convex corpus adiposum ["melon"]. The dorsum, forehead, and upper caudal crest are black with two long gray fields stretching along the flanks below these black fields; the ventral side is white. This animal does not blow fountains [i.e. its blows are thin] and exhibits much of its body in normal movements. It often leaps completely clear of the water. In rapid movement, white surf forms along the body flanks. Schools of different strengths are common. Sometimes the herds merge into congregations of many thousands of animals. (V.A.)

Economic Importance

Only the Black Sea common dolphin has been of commercial importance and in times past was caught in large numbers. In all the remaining

sections of its range, this species has never attracted special interest and was caught in very small numbers.

Hunting the Black Sea dolphin is centuries old. For many years Turkish hunters used an extremely primitive method in killing them. Hunting activity intensified only after the October Revolution. The first cartel for this purpose was organized in 1929 in the Crimea. At this time, along with the then-prevailing method of hunting with firearms, dolphins were also caught in sweep nets. Hunting with firearms was carried out from ships using a smooth-barreled gun and buckshot. Since in summer the killed dolphins sank rapidly, expert divers were always onboard who jumped into the water simultaneous with the shot and held the killed dolphin afloat. Nevertheless, many killed dolphins sank and others who were injured probably died subsequently. Therefore hunting with firearms was ultimately banned and further development proceeded by perfecting the use of sweep nets.

After several improvements in catching dolphins in sweep nets in the 470 Black Sea, the following method was adopted. The net, made of fabric, was up to 500 m long (sometimes up to 1,500 m), wall height 60-80 m, and mesh size (diagonally) about 15 cm. Special rings were provided on the lower seine rope of the net through which a rope was run for tightening the bottom of the net (like a purse). A brigade of catchers comprised 30-40 men equipped with one seiner, two or three motorboats, and up to 10 feluccas. The net was held on the stern of the seiner, cast by the moving ship, and drawn up from the water mechanically. The feluccas going out for the catch and returning to the coast, were towed by motorboats. Each felucca had two oarsmen with a sufficient stock of stones.

The seiner and another boat approached a school of dolphins from two sides with a comparatively long distance between them, leaving the feluccas with the oarsmen at equal intervals on the trail. Having swept the school from three sides in the form of a horseshoe, they blocked the fourth side with a small sweep net. Striking stones against each other ("telephoning") and shouting from the feluccas left along the spread out net, the catchers prevented the dolphins from leaving it until the ends of the net could be drawn together. To prevent the net from sagging or twisting in the water current, the hunters on the feluccas positioned along the entire course of the net held onto its upper edge and flexed it in different directions. By drawing the rope running through the rings on the lower side, a "purse" was formed from which the dolphins caught were gathered in by the feluccas and later loaded on the seiner for transporting to the coast. Hundreds of dolphins were often caught in one casting of the net. If another school of dolphins happened to be sighted in the proximity, the brigade began casting a new net without giving up

Table 38. Catch of dolphins in the Black Sea (Bodrov, Grigor'ev, and Tver'yanovich, 1958)

Year	Number of animals caught	Year	Number of animals caught
1931	36,490	1945	3,464
1932	53,858	1946	15,872
1933	67,469	1947	19,400
1934	67,065	1948	20,863
1935	70,448	1949	32,200
1936	62,933	1950	42,535
1937	103,814	1951	20,250
1938	147,653	1952	50,618
1939	81,206	1953	42,757
1940	71,097	1954	82,809
1941	40,250	1955	18,354
1942	1,157	1956	16,082
1943	2,896	1957	29,800
1944	441		

the first catch. Thus the brigades sometimes returned to the coast with catches in several nets. Dolphin hunting was successfully developed in Bulgaria later.

The results of erstwhile dolphin hunts in the Black Sea (in the Soviet Union) are shown in Table 38.

When the catch rapidly diminished in subsequent years, hunting of the Black Sea dolphin was discontinued.

Statistics of the catch of the Black Sea dolphin provide no specieswise classification and hence the proportion of the common dolphin is not ascertainable. The ratio of the different species of dolphins in the Black Sea hunts varied considerably in different years but the following figures could be regarded as averages: number of common dolphin, common porpoise (*Phocoena*), and bottlenose dolphin (*Tursiops*) = 200:10:1. Thus the common dolphin invariably represented the bulk of the animals caught (Tsalkin, 1937).

471 The average weight of a whole dolphin according to long-term data is 51 kg; thus the quantum of products recovered from a dolphin is relatively small.

Weight of body portions and organs of a small female
Black sea common dolphin, kg (Tomilin, 1957)

Total weight	32
Subcutaneous fat	10.98
Hump flesh	3.85

Caudal musculature	2.50
Backbone	2.55
Ribs with musculature in-between	1.85
Adipose body ["melon"]	0.52
Dorsal fin	0.25
Flippers (two)	0.47
Caudal flukes	0.44
Lower jaw	0.48
Tongue	0.17
Brain	0.67
Intestine	0.97
Gullet	0.23
Heart	0.17
Liver	0.60
Lungs (two with larynx)	1.00
Kidneys (two)	0.19
Stomach	0.20
Skull, blood, etc.	3.91

Dimensions and weight of common dolphins
(18 complete and 12 partial weighings)
(Dragunov and Kasinova, 1954)

Body length, cm	119-190	(\bar{x} = 159)
Total weight, kg	22.0-90.5	(\bar{x} = 50.0)
% of total body weight		
Blubber	26.0-44.8	(\bar{x} = 34.4)
Carcass without head and viscera	30.0-46.8	(\bar{x} = 37.4)
Head	8.1-14.8	(\bar{x} = 10.6)
Tail and fins	2.8-5.2	(\bar{x} = 3.9)
Vicera (entire)	9.2-16.2	(\bar{x} = 12.5)
Flesh with carcass	18.6-24.8	(\bar{x} = 23.4)
Bones of carcass (not cleaned)	10.3-17.0	(\bar{x} = 14.0)
Liver	1.4-3.3	(\bar{x} = 2.3)
Heart	0.39-0.86	(\bar{x} = 0.58)
Lungs	1.9-4.1	(\bar{x} = 3.1)
Stomach (without contents)	0.7-1.3	(\bar{x} = 1.0)
Intestine (with contents)	2.1-5.1	(\bar{x} = 3.3)
Kidneys	0.40-1.02	(\bar{x} = 0.65)
Spleen	0.05-0.18	(\bar{x} = 0.10)
Testes	0.5-1.8	(\bar{x} = 1.4)

Brain	1.1-2.0	(\bar{x} = 1.5)
Jaw fat	0.15-0.34	(\bar{x} = 0.25)
Blood and unaccounted losses	0.05-5.3	(\bar{x} = 1.2)

The amount of subcutaneous fat varies significantly depending on the well-being of the animal. In the period of its maximum fattiness (in April or March), the killed dolphin does not sink. The fat in the animal is minimal in August. The fat recovered from the blubber is used in the paint industry, etc. The better quality fat is used as a substitute for medicinal cod liver oil. The hollow lower jaw of the common dolphin contains a small amount of very valuable fat of a different chemical composition. The oil processed from this fat does not solidify in the cold and is used for oiling fine mechanisms. The carcass of the dolphin is used as raw material for producing meat-bone meal for feeding farm animals. High-quality glue is also produced from this raw material. The skin of this dolphin, after appropriate processing, can be used in the shoe industry for making leather boots.

From the viewpoint of the most rational use of the raw material, dolphin hunting is best carried out in the spring and winter months, in the period of maximum fattiness of the animals. With the same number of animals caught then, a greater quantity of products can be recovered.

472 Commencing from 1965, every type of hunting of the Black Sea dolphins has been banned and all the three species inhabiting this water body have been brought under conservation. Similar measures have been adopted in Bulgaria and Rumania. (V.A.)

Genus of Bottlenose Dolphins

Genus *Tursiops* Gervais, 1855

1843. *Tursio*. Gray. List Mamm. Brit. Mus., p.p. XXIII, 105. *Delphinus truncatus* Montagu, 1821, nom. praeocc.

1855. *Tursiops*. Gervais. Hist. Nat. Mamm., 2, p. 323. substituted for *Tursio* Gray, 1843.

1873. *Hemisyntrachelus*. Brandt. Mém. Ac. Imp. Sc., Pétersbourg. Substituted for *Tursio* Gray, 1843. (V.H.)

Medium-size dolphins with a maximum body length of 3.9 m.

The body build is somewhat heavy, with a "beak" of medium length. The high dorsal fin has a fairly deep notch along the posterior margin. The flippers are relatively broad. The lower jaw is slightly longer than the upper one.

The upper portion of the body is dark gray (sometimes light gray), the flanks gray, and the abdomen white (sometimes gray).

The rostrum of the skull is medium in length, longer and narrower in females than in males. The premaxillae and nasal bones are adjacent on the right side of the skull but not on the left. Broad processes join the pterygoid bones which have an oblique notch posteriorly. The teeth are fairly large (up to 10 mm in diameter) and number $\frac{19-28}{19-25} = 76-106$. They are often completely worn down. The sternum consists of three fused sections. Vertebrae 63-65. Ribs 12-13 pairs. Phalangeal formula: I_1-2 , II_{7-9} , III_{5-8} , IV_{2-5} , and V_{1-2} . The 2nd, sometimes the 3rd digit, is the longest.

These dolphins are benthic-ichthyophagous. Periods of mating and parturition are prolonged. Gestation extends for 11 months while lactation apparently continues for 4-6 months.

These dolphins are distributed in the Atlantic Ocean from the North and Norwegian seas to the Mediterranean and Black seas and South Africa in the east and from southern Greenland to Patagonia in the west; in the Pacific Ocean, from California in the east and Japan in the west to Chile and Australia and New Zealand; and, in the Indian Ocean, from Australia to Africa.

Fossils have been traced to the Upper Pliocene of Europe.

The genus comprises a single species, the bottlenose dolphin, *T. truncatus* Montagu, 1821. Sometimes, one other species, *T. gilli* Dall, 1873, or even six more species are recognized. Apart from *T. gilli*, the five others are *T. nuuanu* Andrews, 1911; *T. aduncas* Ehrenberg, 1833; *T. parvimanus* Reinhardt, 1888; *T. gephyreus* Lahille, 1908; and *T. abusalam* Ruppell, 1842. (V.S.)

BOTTLENOSE DOLPHIN

Tursiops truncatus Montagu, 1821

1780. *Delphinus tursio*. Fabricius. Fauna groenlandica, p. 49, Greenland. The name has no nomenclatural importance since its applicability to this species could not be established.
1804. *Delphinus nesarnak*. Lacépède. Hist. Nat. Cétacées, p. XLIII, 307. Northern Atlantic (nom. praeocc).
1821. *Delphinus truncatus*. Montagu. Mém. Wernerian Nat. Hist. Soc. 3, p. 75. Devonshire, England.
- 473 1832. *Delphinus aduncus*. Ehrenberg. In: Hemprich et Ehrenberg. Symbolae physicae, Mammalia, 2. Red Sea.
1873. *Tursiops gillii*. Dall. Proc. California Ac. Sc., 5, p. 13. Monterey, California.
1911. *Tursiops nuuanu*. Andrews. Bull. Amer. Mus. Nat. Hist., 30, p. 233. Gulf of California.

1940. *Tursiops truncatus ponticus*. Barabash-Nikiforov. Cetacean fauna. Black Sea, p. 56. Novorossiisk, Black Sea. (V.H.)

Diagnosis

Only species of the genus.

Description

Two color groups are recognized among bottlenose dolphins of the Black Sea (Barabash-Nikiforov, 1940, 1960). Type A is characterized by a fairly distinct boundary between the dark color of the dorsum and the white color of the abdomen with a light-colored angular patch in the dark field midbody; the apex of the patch is turned toward the dorsal fin (Fig. 255). In type B, the boundary between the pigmented upper and lower surfaces is not distinct and appears as vague straight, wavy, or broken line, without the light-colored angle near the dorsal fin. The quantitative ratio of animals of the two types varies in different years. Among 50% of the bottlenose dolphins of the two types, a frontopectoral line joins the eyes and gradually extends from their outer corners toward the flippers. Among the bottlenose dolphins of the Atlantic, the light-colored patch characteristic of type A and the frontopectoral line are invariably absent. The latter can, however, be seen in the dolphins of the Mediterranean Sea.

Cervical vertebrae 7, thoracic 12-14, lumbar 17, and caudal 26-27. The cervical vertebrae may be fused in various combinations.

The main body dimensions (as percentage of body length) of bottlenose dolphins averaged for 52 adult animals with a body length of 270-310 cm (Barabash-Nikiforov, 1940) are: distance from tip of lower jaw to base of flippers 18.5, from tip of upper jaw to blowhole 14.0, from

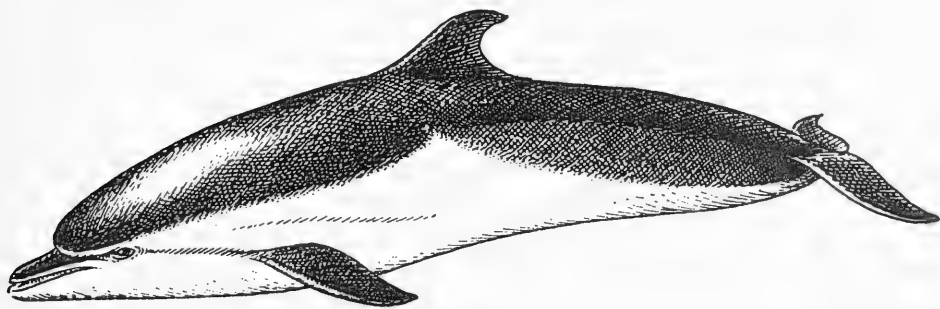


Fig. 255. Bottlenose dolphin, *Tursiops truncatus* (figure by N.N. Kondakov).

tip of upper jaw to commencement of dorsal fin 42.7; length of flippers 14.6; length of dorsal fin 15.6; and width of the left caudal fluke 9.6.

The average length of males caught in the Black Sea was 228 cm, of females 222 cm; the largest male caught was 310 cm long. Bottlenose dolphins from other regions are larger than their Black Sea counterparts: in the waters of Japan, the males average a length of 2.7 m and females 2.8 m; bottlenose dolphins in the Atlantic Ocean attain a length of 3.1–3.3 m and in the Mediterranean Sea 3.2 m. With advancing age, a relative reduction (as percentage of body length) is noticed in the length of the oral slit, length of flippers, and distance from tip of snout to eye and up to the flippers (Barabash-Nikiforov, 1940).

The average main skull measurements of 10 male bottlenose dolphins from the Black Sea with a body length of 180–310 cm and five females with a body length of 214–234 cm (Tomilin, 1957) are respectively: condylobasal length 44 and 44, zygomatic width 23 and 22, length of rostrum 24 and 24, width of rostrum at base 12 and 12, and length of lower jaw 36 (three measurements) and 40 (two measurements).

The skull of the Black Sea bottlenose dolphin is smaller compared to bottlenose dolphins residing in other seas (Fig. 257). Vertebral sections comprise (as percentage of length): cervical 3, thoracic 23, lumbar 30, and caudal 44 (Slijper, 1936). (V.S.)

Geographic Distribution

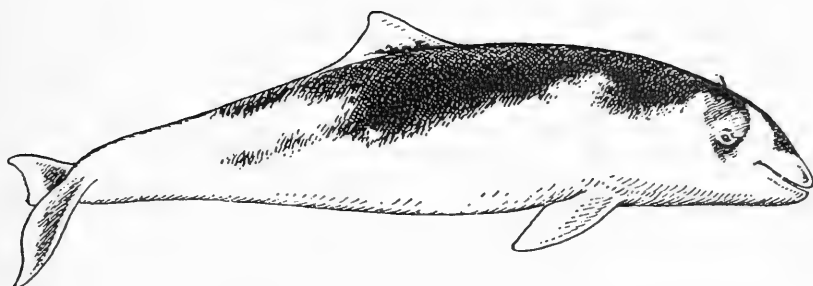
Seas of the temperate and warm belts in the Northern and Southern hemispheres.

Geographic Range in the USSR

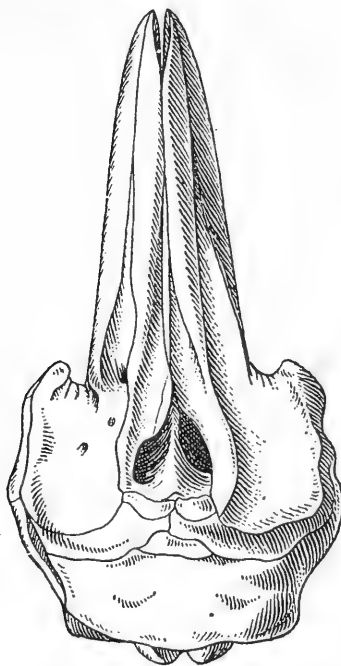
Baltic Sea from Gulfs of Riga and Finland, Barents Sea east to Novaya Zemlya, and the Black Sea; Pacific Ocean Basin, the Sea of Japan, southern part of the Sea of Okhotsk, and waters of the southern half of the Kuril range (Fig. 258).

Geographic Range outside the USSR

In the Atlantic Ocean, in the zone of influence of the Gulf Stream, the range extends north up to the Lofoten Islands on the coasts of Norway, coasts of Iceland, Jan Mayen, and south of Greenland (Fig. 259). In the south, it extends along the African coasts right up to South Africa and into the Mediterranean Sea. Along the west coast of the Atlantic Ocean, this dolphin probably inhabits the waters from Newfoundland to Florida and the Gulf of Mexico and beyond, along the



474 Fig. 256. Embryo of a partly albino bottlenose dolphin, *Tursiops truncatus* (figure by N.N. Kondakov).



474 Fig. 257. Skull of the bottlenose dolphin, *Tursiops truncatus* (figure by N.N. Kondakov).

477 coasts of Argentina, Uruguay, and Brazil. The bottlenose dolphin resides in the waters of the Indian Ocean (Arabian and Red seas, Bay of Bengal, and Seychelles Islands), south up to the coasts of Tasmania and Australia. In the Pacific Ocean, it is encountered on the coasts of the

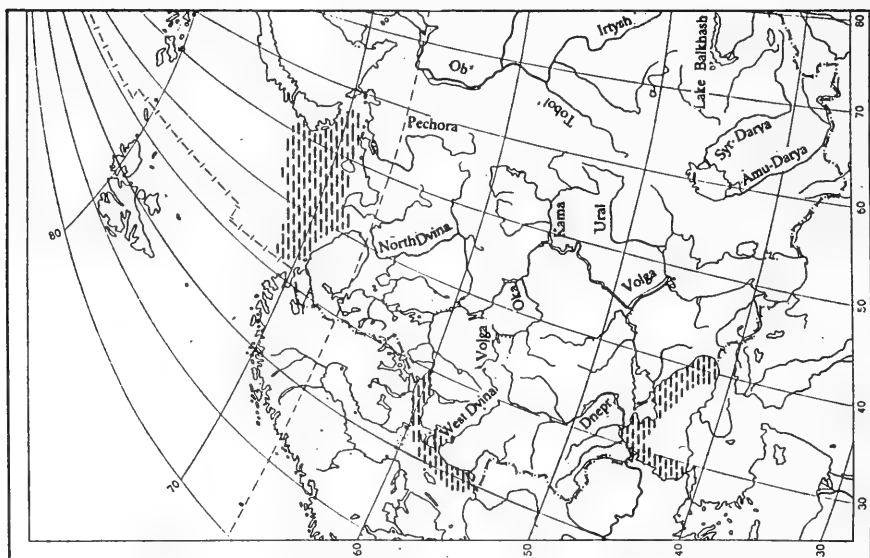
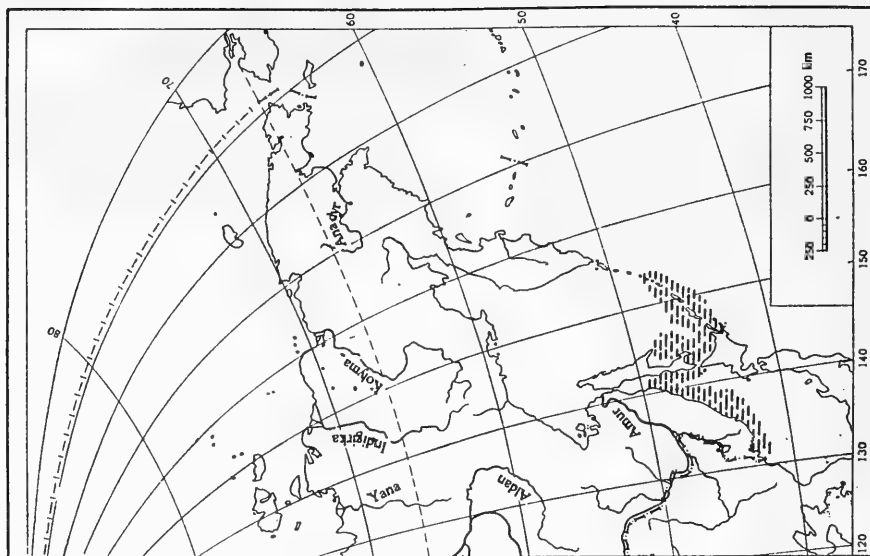


Fig. 258. Range of the bottlenose dolphin *Tursiops truncatus* in the USSR (V.A. Arsen'ev).

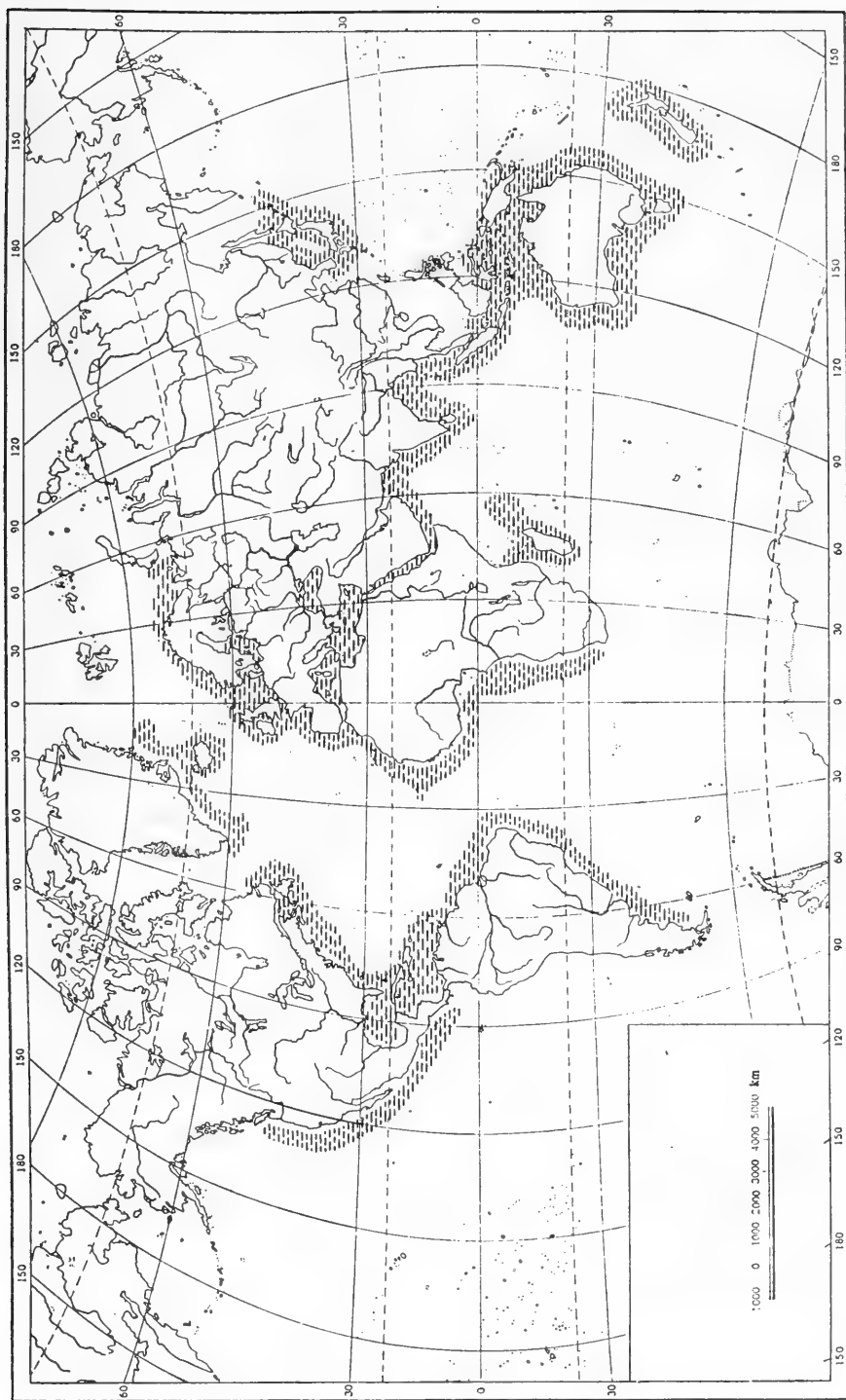


Fig. 259. Species range of the bottlenose dolphin, *Tursiops truncatus* (V.A. Arsen'ev).

Korean Peninsula and Japan, on the coasts of North America (Oregon and California states), and Mexico. In the south, it reaches Australia and New Zealand. No information is available for the Pacific Ocean coast of South America (Sergeant and Fisher, 1957; Tomilin, 1962). (V.A.)

Geographic Variation

Geographic variation has not been adequately studied. Apparently three subspecies are encountered in the waters of the Soviet Union.⁷ These are:

1. **Atlantic bottlenose dolphin**, *T. t. truncatus* Montagu, 1821.

This is the largest form, with body length reaching 390 cm and skull length 550-579 mm. The depression on the lower surface of the frontal bone is inconspicuous. The number of teeth is more than in the other subspecies, usually 21-26 pairs in the upper jaw and 20-25 pairs in the lower.

This subspecies is found in the Baltic and Barents seas and in the waters of the North Atlantic Ocean.

2. **Black Sea bottlenose dolphin**, *T. t. ponticus* Barabash, 1940.

In body and skull dimensions, it is the smallest. Its body length does not exceed 310 cm while the skull length may reach 503 mm. The teeth vary in number from 19-22 pairs in the upper jaw and 18-21 pairs in the lower. The rostrum is shortened and broadened at the base. Broadening and dilation in the midportion of the premaxillae are faintly manifest or altogether absent.

This subspecies is found in the Black Sea.

Outside the USSR, it has been reported in waters south and west of the Black Sea.

3. **Far-eastern bottlenose dolphin**, *T. t. gillii* Dall, 1873.

In dimensions, it probably occupies an intermediate position with the skull length reaching 540 mm. The articulation for the mandibular condyle is very large. The lower surface of the frontal bone is deeply concave anterior to the optic canal. The rostrum is relatively long and narrow at the base.

This subspecies is found in the seas of Japan and Okhotsk and waters of the southern part of the Kuril range.

Outside the USSR, it has been reported in the Pacific Ocean, at least in the northern half. (V.A.)

⁷ Diagnosis of the subspecies after A.G. Tomilin (1957) requires verification and supplementation.

Biology

Population. This dolphin is quite rare in the North Atlantic and Pacific oceans. It is comparatively less in number in the Black Sea, especially compared to the large schools of common dolphins.

Food. Information on food in the Atlantic and Pacific oceans is fragmentary. Fishes serve as the main food, including eels, gray mullets, and small sharks. Bottlenose dolphins examined from the Mediterranean Sea contained the remnants of cuttlefish. More complete information is available about the food objects of the Black Sea bottlenose dolphin. The diet includes many species of fish, crustaceans, and mollusks: haddock, flounder, skate, umbrinas, scorpionfish, anchovy, mullets, gray mullet, Black Sea shad, and bonito; shrimps and isopods; *Nassa reticulata*, *Cardium* sp., *Modiola phaseolina*, *Syndesmia* sp., *Cardium simile*, and *Mytilus* sp. Mollusks are probably not consumed by the bottlenose dolphin but enter the stomach together with sand and gravel, invariably present in large quantity. It is also quite possible that the crustaceans found in the stomach of these dolphins had been priorly ingested by the fish the animals consumed.

Haddock, followed by flounder, is the most abundant fish found in the stomach of bottlenose dolphins. Anchovies, during the period of their en masse concentration, also play a significant role in the dolphin's diet, sometimes even occupying a favored position. All other species of fish play only a secondary role. Thus the bottlenose dolphin is, for the most part, benthophagous since pelagic fish, which even form massive concentrations (anchovy), are consumed more rarely (Kleinenberg, 1936, 1938, 1956a).

Data on the quantum of food intake of the bottlenose dolphin (under natural conditions) are not available. A bottlenose dolphin held captive in a Florida aquarium consumed 20 kg of fresh fish every day while adults in a New York aquarium could manage with 32 kg of fish each (Tomilin, 1957).

Daily activity and behavior. It was earlier assumed that bottlenose dolphins feed only at night but the stomach of those caught during the day contained partly digested food. This led to the conclusion that there are no obvious changes in their diurnal activity (Kleinenberg, 1956a).

Bottlenose dolphins do not form large schools (Fig. 260). They are usually found in groups of ten or a few tens, and only rarely in hundreds. Sometimes the animals produce blows rising to a height of 1-1.5 m. The respiratory pause in an animal moving undisturbed averages 15-17 sec. Feeding dolphins rise to the water surface at irregular intervals, ranging from 5 sec to 2 min, while inhalation/exhalation extend



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Fig. 260. Bottlenose dolphin at sea (photograph by D.A. Morozov).

for 1-2 sec. Sometimes the bottlenose dolphin remains under water for 4 or even 6-7 min. It can dive to a depth of 50-90 m (possibly even to 150 m) at speeds varying from 3-5 to 11-13 km/hr, with a maximum of 30-40 km/hr. Sometimes the bottlenose dolphin breaches the water, "rising" to heights of over 3-4 m (Tomilin, 1957, 1962).

Cases of active cooperation have been observed among these dolphins. On October 30, 1954, an adult dolphin in a herd of some 25 animals was stunned by a dynamite explosion off the coast of Florida. Immediately, two large dolphins came to its rescue, lifted it from under the flippers, and supported it on the water surface. The rescuers periodically dived and surfaced and throughout this period the entire group moved in a wide arc. The operation gave the impression that the pair of supporting animals interchanged since the rest of the animals remained in their proximity. After a few minutes, the affected dolphin began to recover and the entire school then quickly moved away from the ship. Every 10-20 sec, the dolphins breached the water, flying in the air for 7-9 m.

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In another incident, recorded on November 23, 1954, also in Floridan waters, some dolphins that had been caught were being transferred from a ship into a specially constructed tank. Three adult animals had already acclimatized well while the fourth on being lifted from the deck by the tail struggled fiercely and hit its head against the wall of the tank. The

dolphin was stunned and sank to a depth of 2 m. Two of the already transferred dolphins quickly rushed, as in the previous case, to hold and support it on the surface of the water until the affected animal's respiration normalized. Thereafter the two rescuers returned frequently to the bruised animal, abandoning it only after it had begun to swim freely without their assistance. The third dolphin had meanwhile remained in the proximity of the others (Siebenaler and Caldwell, 1956).

The bottlenose dolphin can survive in captivity better than other species, live long in large aquariums, is easily trained, and often raises offspring in captivity. Sometimes a conditioned reflex can be developed in a dolphin within a week's time by repeating the stimulus no more than two or three times, after which a new stimulus can be introduced. The bottlenose dolphin learns quickly to jump through a hoop, tug a boat or a raft, play with a ball, etc. The dolphins are usually held in tanks in groups, eat well, and sleep well. They often sleep at night and in the morning, occasionally enjoying a siesta after a meal.

They produce different types of sounds in the frequency range of 7,000 to 170,000 Hz: whistling, howling, barking, clapping of jaws, etc. Each sound has a particular meaning, relevant to feeding, excitement, mating, fright, etc. (Tomilin, 1962).

Seasonal migrations and transgressions. On the European and American coasts of the North Atlantic Ocean, bottlenose dolphins probably perform regular migrations but no direct observations have been reported. In the Black Sea, they inhabit only the coastal shallow water zone and are never seen in the open sea. They are most often seen in the northeastern part of the Black Sea along the coasts of southern Crimea and northern Caucasus but have been sighted in small numbers in other parts of the sea as well. During the migration of Azov anchovy, bottlenose dolphins form schools that are larger than at any other time and concentrate in the fore-channel zone of the Black Sea and are seen even in Kerch Strait. However, they do not enter the Azov Sea. Apparently, the Black Sea bottlenose dolphin does not undertake regular migrations (Kleinenberg, 1956a).

Reproduction, growth, and development. The period of reproduction is highly protracted although most calves are born in the warm season of the year. However, in a Florida aquarium, four calves were born in February, one in March, one in April, and four in May (Tomilin, 1962).

Thirty-four females caught in November were accompanied by suckling calves and the mammary glands of the mothers held milk. Gestation extends for 12 months. In 1953, in a marine aquarium, a female in the company of a male from February 23 through March 9 underwent parturition on March 4, 1954. Some other observations confirm the 12-month



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Fig. 261. Parturition in the bottlenose dolphin, *Tursiops truncatus* (figure by N.N. Kondakov).

cycle of gestation (Tavolga and Essapian, 1957). Large embryos (Fig. 261) measured 90 to 130 cm in length while two newborn calves were 122 and 124 cm long (Barabash-Nikiforov, 1940). According to observations on captive dolphins, calves were born under water tail first, with formed dorsal fin and caudal flukes. Immediately after whelping, the mother swirled about in the tank, thereby readily separating the umbilical cord. The newborn swam slowly along the waterline, inclined to the surface, and took its first breath 10 min after birth. After 1 hr and 45 min, it suckled milk for the first time. According to other observations, subsequent feedings proceed day and night at intervals of 15-30 min.

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The females in an advanced stage of pregnancy segregate from the herd and form a separate group of pregnant animals. After parturition, the mother as well as the other females living in the proximity protect the calf by turns from possible attack by males. For a few weeks, the mother does not allow her calf to swim for more than two-three meters out of her sight. The duration of lactation apparently varies markedly. In one case, the calf was milk-fed for 3.5 months while another calf was found to partake of a fish by itself just seven months after birth. Yet a case is known of a young dolphin continuing to suckle its mother for 18 months (Tavolga and Essapian, 1961*; Tomilin, 1962).

Growth rate has not been established. Apparently the newborn grows rapidly on the high fat content of the mother's milk, which in composition contains: fat 46.1%, protein 11.55%, sugar 1.57%, dry residue 13.5%, ash 0.38%, and water 40.5% (Ural'skaya, 1957).

A female born in a marine aquarium was fertilized for the first time at six years of age and the first calf born a year later. Considering the duration of gestation and lactation, it may be assumed that the bottlenose dolphin has a two-year reproductive cycle. A female born in a Florida aquarium gave birth to four calves over a 15-year period. A male when caught was approximately 1.5-2 years of age with a body length of 183 cm; he lived in the marine aquarium for six years and ten months and grew in this period to 231 cm, i.e., added 48 cm in almost seven years (Sergeant, 1959b).

Enemies, diseases, parasites, mortality, and competitors. The killer whale can be an enemy of the bottlenose dolphin, as also of other dolphins. The diseases affecting the bottlenose have not been investigated. In a Florida aquarium, two dolphins died of infectious erysipeloid (pathogen: *Erysipelothrix rhusiopathiae*). In a New York aquarium, instances of pneumonia were recorded. Skeletal diseases were also reported (Tomilin, 1957).

A female bottlenose dolphin measuring 266 cm long and weighing 180 kg was caught in the waters of Japan in July, 1954 and placed in a tank. In December of the same year, many nodular formations were noticed on her skin, the animal became debilitated, and a month later died. The affliction turned out to be a bacterial fungal infection caused by a parasite of the genus *Trichophytum* Malm. Acute pneumonia was also reported in this dolphin (Hoshina and Sugiura, 1956).

Eleven species of helminths have been reported in the bottlenose dolphin: three trematodes, three cestodes, four nematodes, and one species of acanthocephalan. The trematode *Braunina cordiformis* Wolf, a parasite of the stomach and intestine of the bottlenose dolphin, was also found in the common dolphin and one species of spotted dolphins in the Adriatic Sea, in the region of Rio de Janeiro, and in the waters of California and Panama. Another species of trematode, *Synthesium tursionis* Marchi, was detected in the intestine of only the bottlenose dolphin in European waters. In a Californian aquarium, the bile ducts of the liver of a bottlenose dolphin revealed *Zalophotrema hepaticum* Stunkard and Alvey, known earlier from the Californian sea lion.

The cestode *Phyllobothrium delphini* Bosc, parasitizing the skin and subcutaneous tissue, is widely distributed among marine mammals. Besides the bottlenose dolphin, it is found in the bowhead whale,

six species of toothed whales, and one species of seals. It has been detected in the Atlantic and Pacific oceans, Mediterranean Sea, and in the waters of Australia and Antarctica. In the bottlenose dolphin and four other species of dolphins, the cestode *Monorygma grimaldii* Monier parasitizes the abdominal cavity, mesentery, and diaphragm; it has been detected in the Atlantic Ocean and the Mediterranean Sea. The third species of cestode belongs to the genus *Diphyllbothrium* (species not established).

Of the four species of nematodes, *Anisakis turionis* Gruz was detected in the bottlenose dolphin from the Indian Ocean. *Crassicauda crassicauda* Creplin, parasite of the urogenital system, was found in beaked whales and six species of baleen whales, in addition to the bottlenose dolphin; it was detected in the Atlantic Ocean in the Northern and Southern hemispheres. The nematode *Halocercus lagenorhynchi* Baylis and Daubney is a parasite of the lungs (bronchi) of the bottlenose dolphin and the white-beaked dolphin; it was detected on the European coast of the Atlantic Ocean and in the waters of Australia. *Stenurus ovatus* Linstow was detected in the blowhole, bronchi, and blood vessels of only the bottlenose dolphin in the Mediterranean and Black seas. Forty-one larvae of the nematode genus *Anisakis* were found in a female bottlenose dolphin caught in the waters of Japan, probably the larvae of *Anisakis catodonis* Baylis (Hoshina and Sugiura, 1956). The only species of acanthocephalans localizes in the intestine of the bottlenose dolphin *Corynosoma cetaceum* Johnston, and has also been found in the common dolphin in the waters of Australia (Delamure, 1955).

The natural mortality of the bottlenose has not been studied. Some other species of dolphin feed on the same diet and constitute food competitors.

Field characteristics. Adults usually measure 220 to 250 cm. They are dorsally and ventrally light in color; the transition in coloration is gentle, with no sharp demarcation between the two. Body movements are placid. It neither splashes water while swimming nor does it breach high. (V.A.)

Economic Importance

In the recent past, several hundreds of bottlenose dolphins were caught every year in the Black Sea. In other regions, where many other species of dolphins were caught, the bottlenose constituted a negligible percentage of the total catch. Various types of nets were used to catch it
482 along with other dolphins. The weight of the animals ranged from 90 to

almost 200 kg, of which the skin with the fat accounted for 30% and the flesh 33%. An analysis of the seasonal catch of the Black Sea bottlenose dolphin showed that the average weight of the dolphin was 175 kg, of which the subcutaneous fat was 50.8 kg (29%) and the skin 7 kg (4%) (Dragunov and Kasinova, 1951).

The total quantum of products obtained from bottlenose dolphins caught all over the range was extremely meagre. Hunting of the bottlenose dolphin, and of other species of dolphins as well, has been banned in the Black Sea. (V.A.)

Genus of Right Whale Dolphins

Genus *Lissodelphis* Gloger, 1841

1830. *Tursio*. Wagler. Nat. Syst. Amphibien, p. 34. *Delphinus peronii* Cuvier. Nom. praeocc.

1841. *Lissodelphis*. Gloger. Gemein. Naturgesch, 1, p. 169. *Delphinus peronii* Lacépède, 1804.

1846. *Delphinapterus*. Gray. Zoology. Voyage Erebus and Terror, 1, p. 36. *Delphinus peronii* Lacépède. Nom. praeocc. (V.H.)

Small dolphins, with a body length of up to 2.4 m.

Table 39. Weight of body parts and organs of bottlenose dolphin from the Black Sea (in March), kg (percentage of total weight shown in parentheses) (Okuneva, 1934)

Total weight	143.53	(100.0)
Head	12.0	(8.36)
Flippers and dorsal fins	2.06	(1.43)
Caudal flukes	2.09	(1.45)
Skin	6.0	(4.11)
Carcass fat	46.0	(32.11)
Flesh (muscles)	39.9	(27.17)
Bones (trunk skeleton)	17.0	(11.83)
Brain	1.46	(1.01)
Tongue	0.37	(0.25)
Lower jaw	0.79	(0.55)
Upper jaw	1.09	(0.76)
Viscera, including:	17.3	(12.05)
Liver	2.7	(1.88)
Heart	0.67	(0.46)
Lungs	4.5	(3.13)
Stomach	1.55	(1.08)
Intestine	7.2	(5.01)
Kidneys	0.68	(0.47)

The body is highly elongated and well proportioned. The head, with a low and inclined forehead gradually passes into the relatively short "beak". The "beak" is set off from the adipose body of the forehead by lateral furrows. The flippers are crescent-shaped. A dorsal fin is lacking. Caudal flukes are relatively small. The lower jaw is slightly longer than the upper.

The body is black above and whitish below and the boundary between the upper and lower body colors is very sharply defined.

The rostrum is broad and slightly longer than the cranium. The pterygoid bones are not adjacent. The premaxillae are flattened anteriorly. The mandibular symphysis is short, less than one-fifth the jaw length. The teeth are small and number $\frac{40-47}{42-49}$. The scapula, almost semicircular in form, has prominent coracoid and acromion processes. Cervical vertebrae 7, thoracic 14-17, lumbar 29-33, and caudal 35-40; total 88-92.

The biology of this genus is hardly known but apparently these dolphin species feed mainly on fish and cephalopods.

Information on the distribution of this genus is very inadequate and sketchy: Atlantic Ocean around South Africa and south of southern Brazil in South America, Pacific Ocean along the coasts of Chile, north up to 37° N lat., and from Tasmania and New Zealand (evidently Australia too) north up to New Guinea, and in the North Pacific Ocean from the Bering Sea south to California and Japan.

The genus comprises two species: the southern right whale dolphin (Peron's dolphin), *Lissodelphis peroni* Lacépède, 1804, and the northern right whale dolphin *L. borealis* Peale, 1848. Only the latter has been established in USSR waters but the appearance of the southern species is quite likely. (V. S.)

NORTHERN RIGHT WHALE DOLPHIN

Lissodelphis borealis Peale, 1848

1848. *Delphinapterus borealis*. Peale. U. S. Explor. Exped. 8, p. 35, 10° west of Astoria, Oregon, USA; 46° 6' 50" N lat. and 134° 5' E long. (V. H.)

Diagnosis

The body length, up to 2.4 m, is maximum for the genus. For a description of the external features, see under the characteristics of the genus. Typically, the body is almost entirely black. A narrow light-colored band runs only on the ventral side from the throat to the tail and forms a

483 rhomboid patch between the flippers. The upper side of the beak, part of the forehead, and tip of the lower jaw may also be white (Fig. 262). For skull characteristics, see under the description of the genus. Phalangeal formula: I_{1-2} , II_8 , III_9 , IV_3 , and V_{2-3} . (V.S.)

Description

The upper side of the caudal flukes is black but partly white or gray on the underside and dark along the margins. The flippers are black.

Teeth $\frac{40-47}{42-49}$.

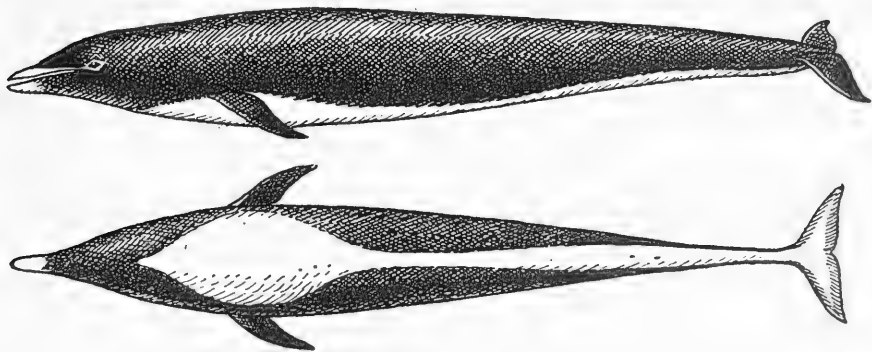
Cervical vertebrae 7, thoracic 14-17, lumbar 29-33, and caudal 35-40; total 88-92. The first two cervical vertebrae are fused.

The body dimensions of four males and seven females caught on the coasts of Japan (Tobayama, Uchida, and Nishiwaki, 1969) are (in cm): body length 145-292 (\bar{x} 204); distance from tip of snout to forehead 3-6 (\bar{x} 4.6), to center of blowhole 22-34 (\bar{x} 30), and to flippers 39-64 (\bar{x} 53); distance from anal opening to notch between caudal flukes 40-70 (\bar{x} 53); length of flippers 24-31 (\bar{x} 28), maximum width of flippers 7.3-9.7 (\bar{x} 8.6); distance between caudal flukes from apex to apex 18-41 (\bar{x} 33); and maximum height of body 20-37 (\bar{x} 30).

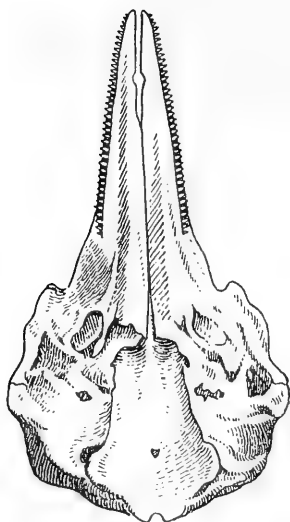
The skull (Fig. 263) dimensions of three male northern right whale dolphins (Tomilin, 1957) of 213, 208, and 246 cm, body length are respectively: condylobasal length 45, 42, and 44 cm; length of rostrum 26, 23, and 24 cm; width of rostrum at base 11, 11, and 11 cm; and length of lower jaw 38, 37, and 38 cm. (V.S.)

Geographic Distribution

North Pacific Ocean.



483 Fig. 262. Northern right whale dolphin, *Lissodelphis borealis* (figure by N.N. Kondakov).



483 Fig. 263. Skull of the northern right whale dolphin, *Lissodelphis borealis* (figure by N.N. Kondakov).

Geographic Range in the USSR

484 Waters of the Kuril Islands (from Shpanberg to Paramushir) but encountered more often from the Pacific Ocean side. Apparently also occurs in the eastern parts of the seas of Okhotsk and Japan (Fig. 264).

Geographic Range outside the USSR (Fig. 265)

Widely distributed in the Pacific Ocean along the American and Asian coasts, in the waters of Honshu and Hokkaido islands, on the coasts of North America from California and Washington states to the Gulf of Alaska and the eastern part of the Bering Sea; residence in the western part of the sea has not been established. (V.A.)

Geographic Variation

Not established. Quite likely the accepted species of this genus are only subspecies of a single species (*L. peroni* Lac.). (V.A.)

Biology

The population of this species is very small over much of its range. Maximum concentration in all probability occurs in the waters of Japan.

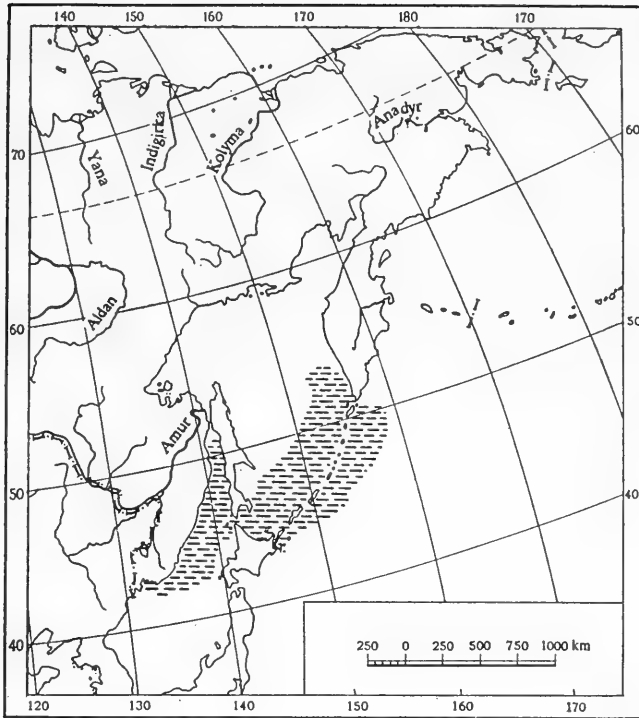


Fig. 264. Range of the northern right whale dolphin, *Lissodelphis borealis* in the USSR (V.A. Arsen'ev).

Fish represent the main food while cephalopods are consumed in small quantities. A female caught on March 28, 1959 east of Honshu Island contained an embryo 43 cm long.

These dolphins live predominantly in small schools far away from the coasts. They leap clear of the water. They exhibit a strong mutual affinity, never abandoning an injured animal and remaining with it for a long time.

In the waters of Japan, the northern right whale dolphin is caught regularly along with other species. At least a few hundred of them are hunted every year. Thus, in May and June of 1949 alone, in the central part of the coastal Pacific Ocean waters of Honshu Island, a whaling company caught 465 of them. Hunting is usually done with rifles, followed by harpooning the injured animal manually. The shooter and the harpoon striker operate on a special wooden platform fitted on the bow of the

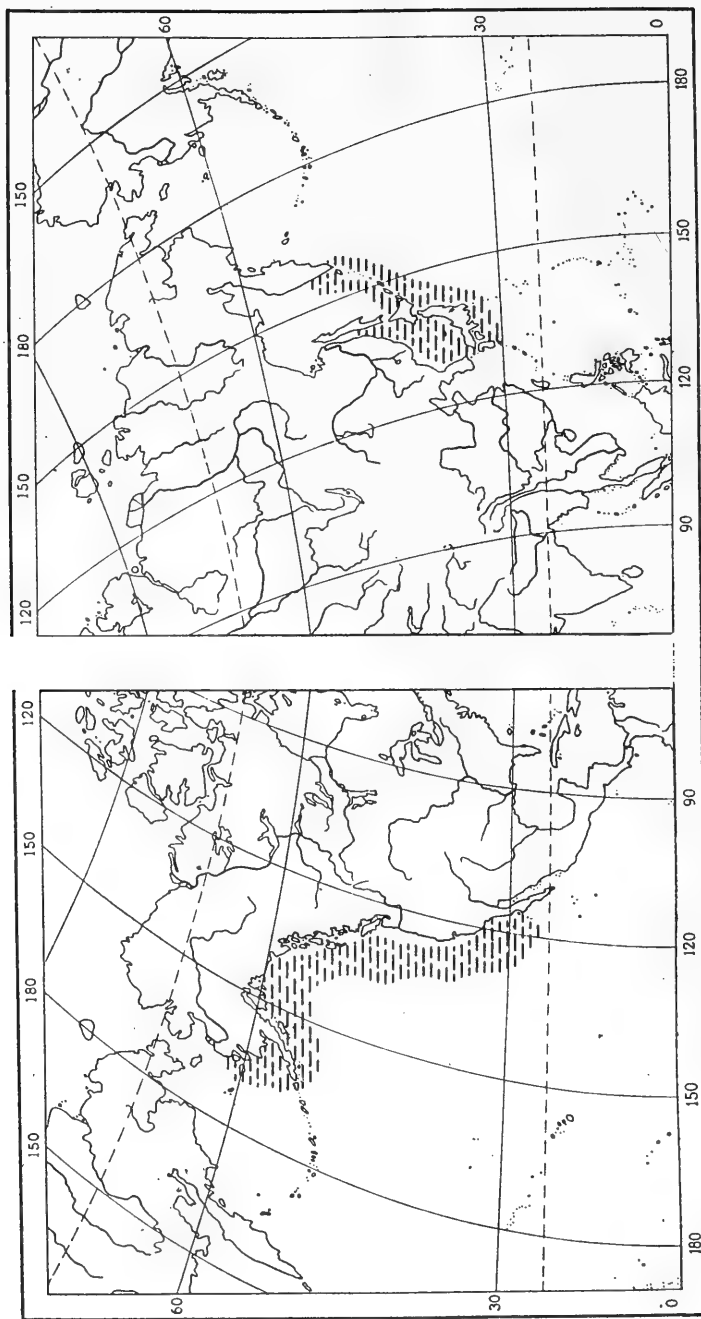
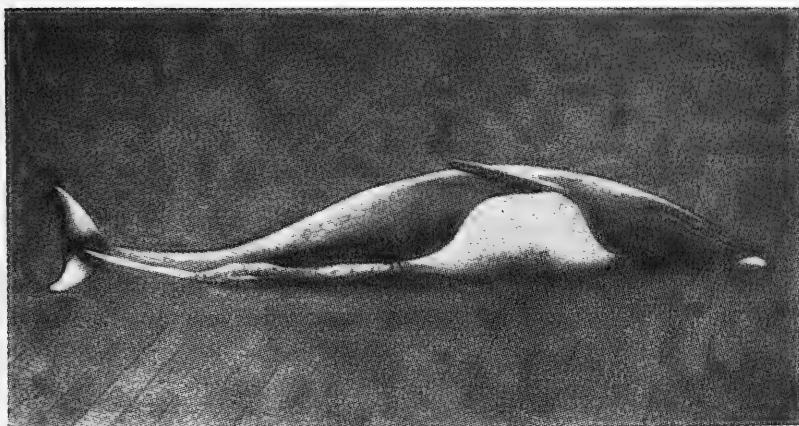


Fig. 265. Species range of the northern right whale dolphin, *Lissodelphis borealis* (V.A. Arsen'ev)



486 Fig. 266. Northern right whale dolphin, *Lissodelphis borealis*, on the deck of a ship. Pacific Ocean east of Honshu Island, 1959 (photograph by G.M. Kosygin).

ship. Ships with a water displacement of 20 to 30 tons and capable of logging 7 to 10 miles per hour are used. The killed dolphins are processed on the deck of the ship (Fig. 266). A ship enjoying a successful hunting expedition returns with a catch of 200 or more dolphins of different species.

An experimental catch of these dolphins using woven nets was carried out near Iturup in the Kuril Islands in September, 1955. The nets were cast over a herd of 25 animals but only 5 were actually caught.

The products of dolphin hunting are marketed in Japan where the liver, heart, and kidneys are consumed. Bones and various remnants are ground into fertilizer meal. Oil is obtained from the blubber. The skin is used in making leather goods (Wilke, Taniwaki, and Kuroda, 1953; Sleptsov, 1955, 1961; Klumov, 1959). (V.A.)

SOUTHERN RIGHT WHALE DOLPHIN (PERON'S DOLPHIN)

Lissodelphis peroni Lacépède, 1804

1804. *Delphinus peronii* Lacépède. Hist. Nat. Cétacées, p.p. XLIII, 316. Tasmanian waters. (V.H.)

These dolphins are smaller than the northern right whale dolphin. The body length of a male caught in waters of Japan was 227 cm (Tobayama *et al.*, 1969). In external features and structure and skull proportions, they in no way differ from their northern counterparts. The typical coloration of the southern species is: black dorsally and on most of the lateral surface, and white on the abdomen and the lower parts of the body flanks (Fig. 267).

The tip of the snout and small sections of the vertical surface of the caudal flukes adjoining the caudal crest are black. The white field covers the level of articulation of the black flippers. The edge of the upper jaw (apart from its apex) and the zone posterior to and below the eyes are white.

Teeth $\frac{44-45}{45}$.

Cervical vertebrae 7, thoracic 17, lumbar 29, and caudal 37; total 90.

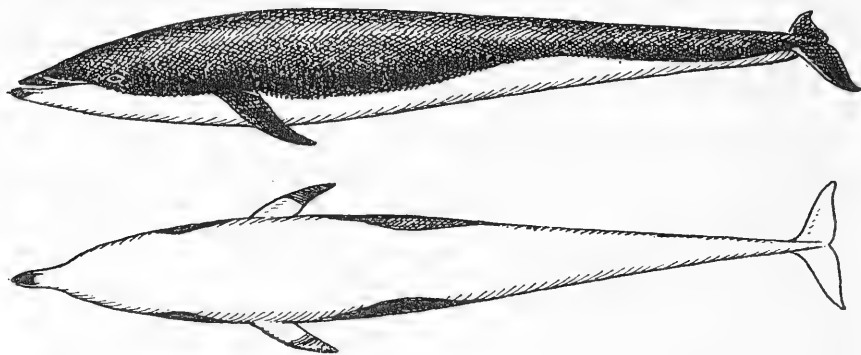
The body dimensions of a male caught on the coasts of Japan (Tobayama *et al.*, 1969) are (in cm): body length 227; distance from tip of snout to forehead 4, to center of blowhole 36, and to flippers 59; 487 distance from anal opening to slit between caudal flukes 61; length of flipper 30, maximum width of flipper 9.5; distance between caudal flukes from tip to tip 38; maximum height of body 27.

The skull (Fig. 268) dimensions of the same specimen are (in cm): condylobasal length 47, length of rostrum 26, width of rostrum at base 12, interorbital width 18, length of lower jaw 40, and length of mandibular symphysis—[48].

Geographic Distribution

Habitation in the waters of the USSR has not been established but residence in or transgressions into the Sea of Japan or waters of the Kuril Islands are possible.

Outside the USSR, it is encountered in the southern part of the range (see under the characteristics of the genus); indicated for the waters of Japan. (V.H.)



487 Fig. 267. Southern right whale dolphin, *Lissodelphis peroni* (figure by N.N. Kondakov).

Biology

Not known. Japanese fishermen from Otsu, Ibaraki Prefecture caught a group of dolphins swimming together on April 1, 1969, which included the southern right whale dolphin, the northern right whale dolphin, and the Pacific common dolphin (Tobayama, Uchida, and Nishiwaki, 1969). (V.A.)

Genus of Shorthead Dolphins

Genus *Lagenorhynchus* Gray, 1846

1846. *Lagenorhynchus*. Gray. Ann. Mag. Nat. Hist., 17, p. 84. *Delphinus albirostris* Gray, 1846.
 1866. *Electra*. Gray. Cat. Seals and Whales Brit. Mus., p. 268. *Lagenorhynchus electra* Gray, 1846. Nom. praeocc.
 1866. *Leucopleurus*. Gray. Proc. Zool. Soc. London, p. 216. *Delphinus leucopleurus* Rash, 1843.

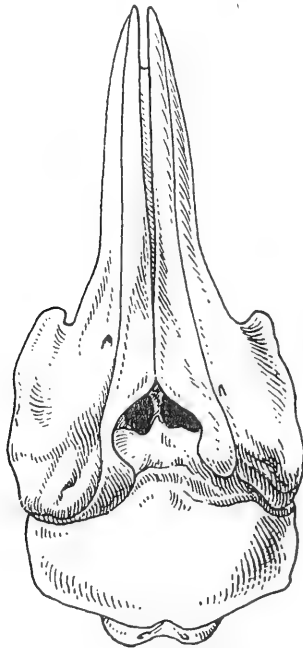


Fig. 268. Skull of the southern right whale dolphin, *Lissodelphis peroni* (figure . by N.N. Kondakov).

1966. *Peponocephala*. Nishiwaki and Norris. Ocean Res. Inst., Univ. Tokyo, 5, 139. *Electra electra* Gray, 1846. (V.H.)

Small dolphins, with a well-proportioned body ranging in length from 1.5 to 3 m.

The "beak" is short, not more than 7 cm; in most of these animals, it is well demarcated from the forehead by a furrow. The high dorsal fin is crescent-shaped and located at the center of the dorsum or slightly anterior to it. A crescent shape is also characteristic of the flippers. Dermal keels run along the dorsal and ventral sides of the caudal stem. The coloration of most of the species is a combination of black, gray, and white fields extending along the body.

The rostrum of the skull is wide at the base and is as long as the cranium or slightly longer. The anterior section of the premaxillae is flattened or slightly concave. The large pterygoid bones adjoin each other or are slightly separated. The length of the mandibular symphysis is less than one-fifth that of the lower jaw. The teeth are small and number $\frac{20-45}{20-45}$. The number of vertebrae varies from 71 to 94 and their centrum is highly flattened. The vertebrae of the lumbar section have very long, thin spinous and transverse processes. The first two or three cervical vertebrae are fused.

Very little is known about the biology of this genus. These dolphins feed mainly on fish and cephalopods. Mating and parturition occur in the summer months.

Shorthead dolphins are distributed in all the oceans in the north up to Greenland and the Barents Sea; in the south they reach the edge of the Antarctic ice (Fig. 269).

The genus apparently comprises six species, although some authors recognize up to ten (Nishiwaki and Norris, 1967): 1) *L. acutus* Gray, 1828; 2) *L. albirostris* Gray, 1846; 3) *L. cruciger* Quoy and Gaimard, 1824; 4) *L. electra* Gray, 1846; 5) *L. obliquidens* Gill, 1865; and 6) *L. thicola* Gray, 1846. *L. electra* is sometimes considered as an independent genus, *Peponocephala* Nishiwaki and Norris, 1966; this aspect calls for further study but it would appear to deserve only a subgeneric rank.

The following species inhabit the waters of the USSR: (1) Atlantic white-sided dolphin, *L. acutus* Gray, 1828; (2) white-beaked dolphin, *L. albirostris* Gray, 1846; and (3) Pacific white-sided dolphin, *L. obliquidens* Gill, 1865. Residence of the broadsnout dolphin, *L. electra* Gray, 1846, is possible.

These animals are not hunted in our waters. (V.S.)

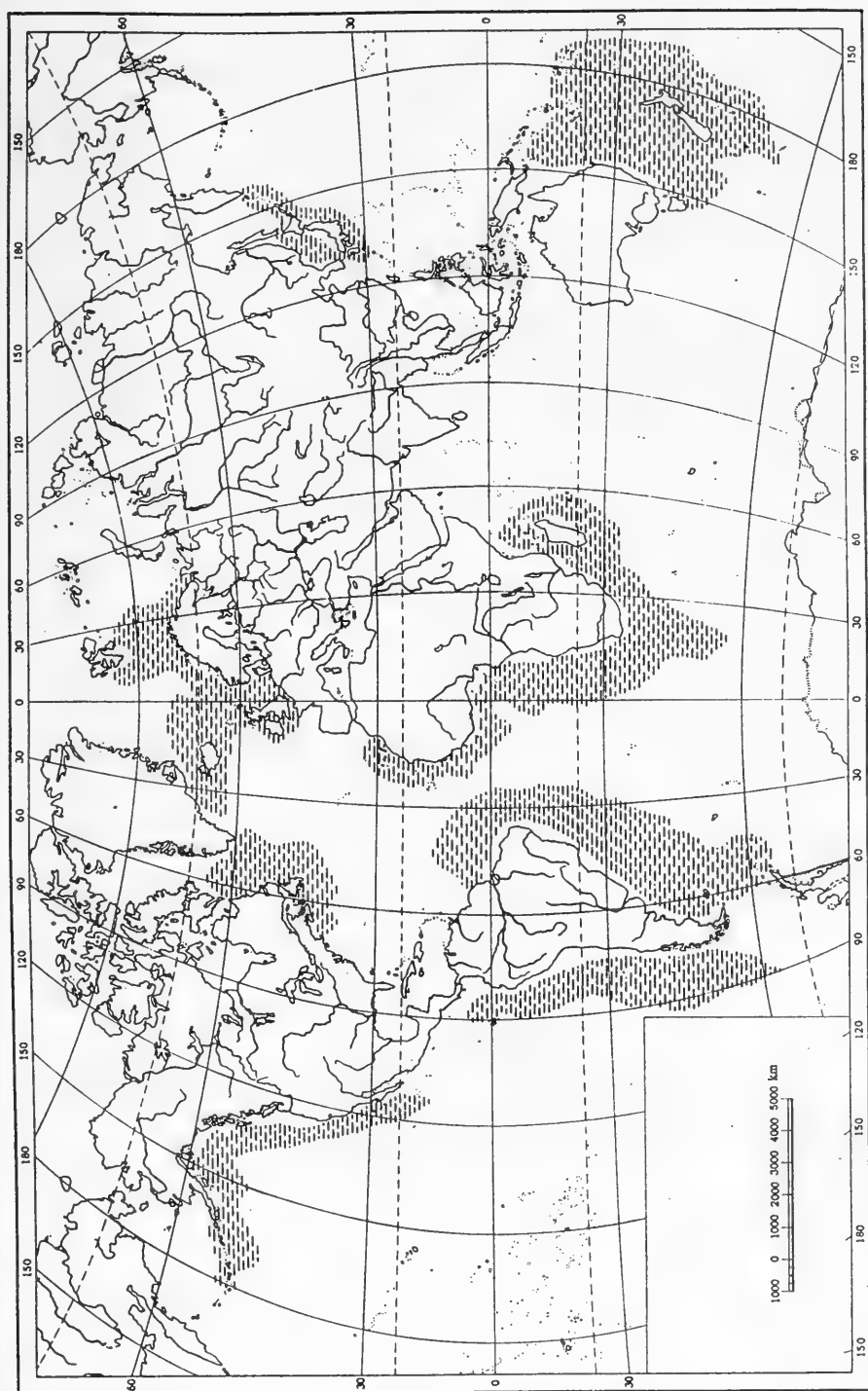


Fig. 269. Range of the genus of shorthead dolphins, *Lagenorhynchus* (V.A. Arsen'ev).

ATLANTIC WHITE-SIDED DOLPHIN

Lagenorhynchus (Lagenorhynchus) acutus Gray, 1828

1828. *Delphinus (Grampus) acutus*. Gray. Spicil. Zoologica, I, p. 2. Faroe Islands.

1843. *Delphinus leucopleurus*. Rash. Nytt. Mag. Natur., vol. 4, p. 100. Kristiana Bay (Oslo), Norway. (V.H.)

Diagnosis

Body length up to 275 cm. The body is mainly black dorsally and on the flanks and whitish ventrally. A broad white band extends along the flanks, roughly from the level of the dorsal fin and almost up to the caudal stem. A narrow black band runs from the base of the flippers anteriorly and upward toward the section between the eye and the corner of the mouth. The dark-colored flippers are surrounded by a white field.

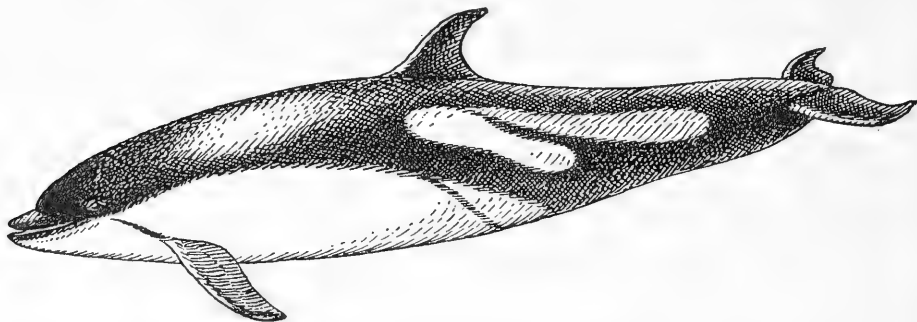
The pterygoid bones are often adjacent in the skull. Teeth $\frac{30-37}{30-37}$. Vertebrae 77-82.

Description

The head is relatively small. The "beak" is not well demarcated from the inclined forehead. The caudal flukes are ventrally light-colored. The margin of the lower jaw is dark-colored. A black ring is seen around the eye and anus (Fig. 270). The embryo bears seven or eight hairs, each measuring roughly 1 cm, on each side of the beak.

The rostrum is slightly longer than the cranial section. The pre-maxillae are flat and their outer edge sinuate. The temporal fossa is elongated.

Cervical vertebrae 7, thoracic 14-15, lumbar 18-22, and caudal 38-41. Phalangeal formula: I_{1-2} , II_{10} , III_6 , IV_{2-3} , and V_2 .



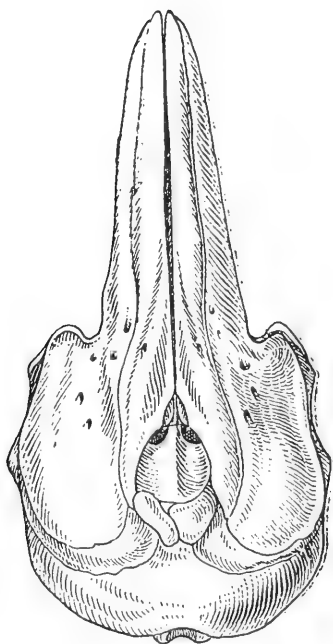
490 Fig. 270. Atlantic white-sided dolphin, *Lagenorhynchus acutus* (figure by N.N. Kondakov).

The body length of an adult female Atlantic white-sided dolphin was 225 cm (Schevill, 1956); distance from tip of snout to commencement of flippers 40 cm, from tip of snout to dorsal fin 87 cm, and from tip of snout to blowhole 29 cm; height of dorsal fin 24 cm, length of dorsal fin along base 34 cm; length of flippers 30 cm; and spread of caudal flukes 65 cm.

The skull dimensions (Fig. 271) (Tomilin, 1957) (average of 10 measurements) are (in cm): condylobasal length 41, length of rostrum 21, width of rostrum at base 11, length of lower jaw (three measurements) 33, and length of mandibular symphysis (two measurements) 43. The rostrum of the skull is shorter than in the Pacific white-striped dolphin but longer than in the white-beaked dolphin. The teeth are usually more numerous than in the other two species but their dimensions are smaller. (V.S.)

Geographic Distribution

North Atlantic Ocean.



Geographic Range in the USSR

Barents Sea up to Spitsbergen and Murman coast of the Barents Sea up to Kanin (Fig. 272). Transgressions are possible into our waters of the Baltic Sea.

Geographic Range outside the USSR (Fig. 273)

In American waters from Davis Strait to the Gulf of Maine (Cape Cod). In the eastern part of the ocean from the Barents Sea (Kanin and Spitsbergen) and southern Greenland to the southern part of the North Sea (England, Belgium, Denmark, and Ireland). In the Baltic Sea, only in the southwest (waters of Denmark, Oslo Fjord, and western coasts to Sweden), in the east not farther than Penemund close to Oder estuary (about 18° W long.) and Koloberg (Poland; Kowalski, 1964).

This species is apparently most numerous on the coasts of Norway, especially in the region of Lofoten Islands and Bergen. Encountered

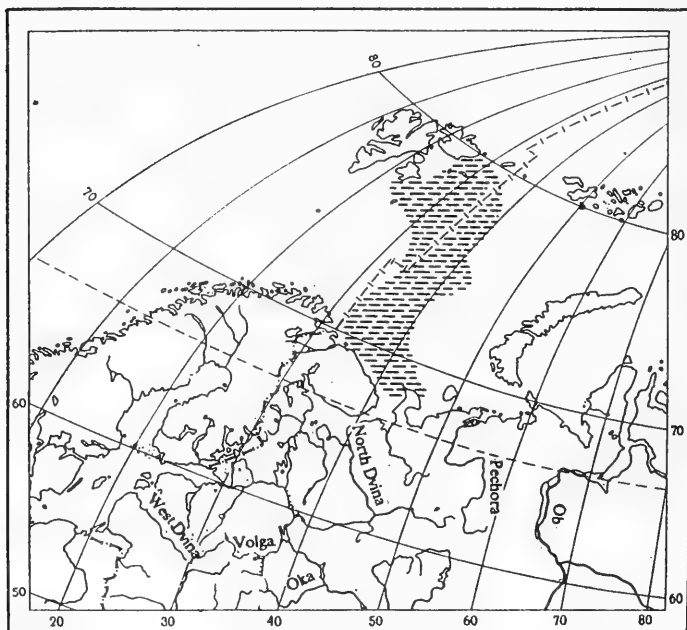


Fig. 272. Range of the Atlantic white-sided dolphin, *Lagenorhynchus acutus*, in the USSR (V.A. Arsen'ev).

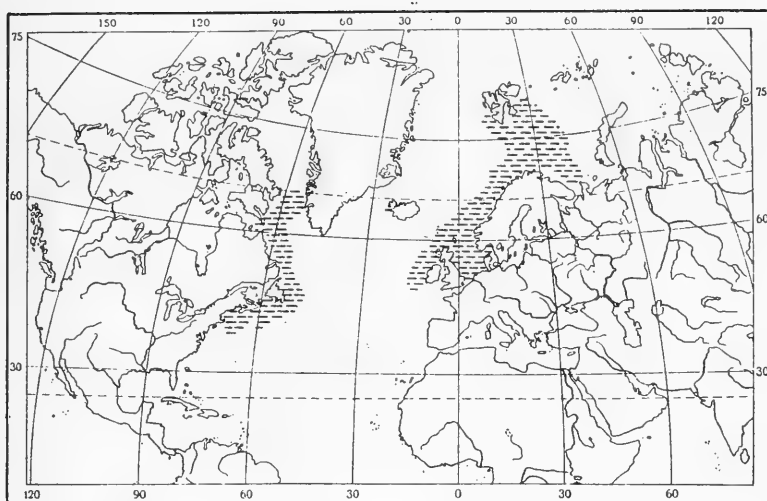


Fig. 273. Species range of the Atlantic white-sided dolphin, *Lagenorhynchus acutus* (V.A. Arsen'ev).

rather often on Faroe and Orkney Islands and on the coasts of Ireland and Iceland (Jonsgard and Nordli, 1952; Tomilin, 1957, 1962). (V.A.)

492

Geographic Variation

Not established.

Biology

Only fragmentary information is available. Pelagic animals are encountered more often than benthic animals in the stomach of these dolphins: salmon, herring, mackerel, and the squid, *Illex illecebrosus*. On one occasion, bottom-dwelling hermit crabs (*Pagurus bernhardtii*) and mollusks (*Buccinum*) were found. It has been suggested that gestation extends for about 10 months and that parturition takes place midsummer since fully mature embryos were found in June. The newborn is 100 cm or slightly more in length, reaching 140 cm by November.

A male 180 cm long proved to be three years old while a female 225 cm long was neither pregnant nor lactating. In Kalvåg Fjord on the west coast of Norway, a school of these dolphins arrived on March 10, 1952 and 52 were caught. Visually, many were about 2.5 m long and the longest about 3 m. About one-third of the dolphins caught contained embryos 55 to 70 cm long. One female contained two embryos, each about 65 cm long.

These dolphins are usually confined to groups of 10 to 50 individuals but at places where fishes concentrate they gather into large schools of 1,000 to 1,500 animals. Migrations have not been traced.

Beached dolphins have been found on the northeastern coast of England, northwestern coast of Ireland, and the coasts of Holland. Once a school of 30-35 animals was found beached on the shoals of Scotland. Beached animals sometimes include both dolphins and pilot whales.

The helminth fauna of the Atlantic white-sided dolphin is rather poor. The nematode *Anisakis (Anisakis) simplex* Rudolphi, wide-ranging in marine mammals, was detected in the gullet, stomach, and intestine. Two species of cestodes were also found: *Strobilocephalus triangularis* Diesing, also parasitizing the intestine of the bottlenose whale and *Mesoplodon* localizes in the abdominal cavity, the mesentery, and the diaphragm. *Monorygma grimaldi* Monier has also been found in three other species of dolphins (Jonsgard and Nordli, 1952; Delamure, 1955; Tomilin, 1957, 1962).

The most characteristic external feature is the broad white band running along the body from both sides below the dorsal fin up to the caudal stem. This band is distinctly visible since it lies between the dark coloration on top and the yellowish-gray color below, the latter covering the lower flanks of the body. The belly of this dolphin is pure white.

This species is of minimal economic importance on the coasts of Norway where up to 1,000 animals are caught in some years. In other regions of the range, it is caught incidentally along with other species. (V.A.)

WHITE-BEAKED DOLPHIN

Lagenorhynchus (Lagenorhynchus) albirostris
Gray, 1846

1846. *Delphinus albirostris*. Gray. Ann. Mag. Nat. Hist., 17; p. 84. Near Great Yarmouth, England. (V.H.)

Diagnosis

Body length up to 304 cm. The color of the upper portion of the body is grayish-black and the underside whitish. The base of the forehead and the "beak" are light gray. The premaxillae are broad and flat and their outer margin is curved. The temporal fossa is ellipsoidal. the pterygoid bones are often adjacent. Teeth $\frac{26-27}{26-27}$ (of these only $\frac{22-25}{22-25}$ are seen above the gums). Vertebrae 88-92. (V.S.)

Description

This species differs from the Atlantic white-sided dolphin in having less developed keels on the caudal stem, very large flippers, and a very high dorsal fin. The flippers and caudal flukes are dorsally dark and somewhat lighter ventrally. The dark color extends down along the flanks of the body and covers the point of articulation of the flippers (Fig. 274).

The rostrum is almost as long as the cranial section.

Usually, the cervical vertebrae number 7, thoracic 14-16, lumbar 24-27, and caudal 43-45. Phalangeal formula: I_{2-3} , II_{6-7} , III_{4-5} , IV_{1-2} , and V_{0-1} . The body length usually varies from 270 to 300 cm.

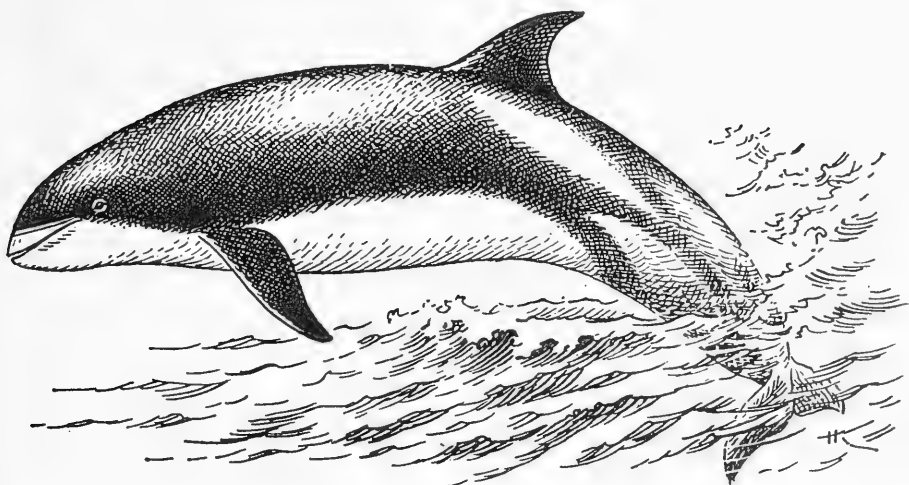
The average main measurements of the skull (Fig. 275) (Tomilin, 1957) are (in cm): condylobasal length 44 (eight measurements), length of rostrum 21 (eight), width of rostrum at base 14 (seven), and length of lower jaw 36 (four). (V.S.)

Geographic Distribution

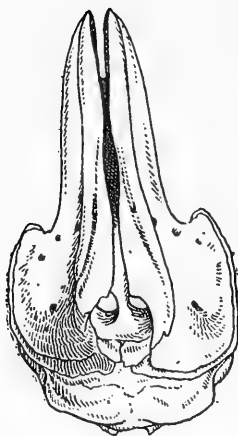
North Atlantic Ocean.

Geographic Range in the USSR

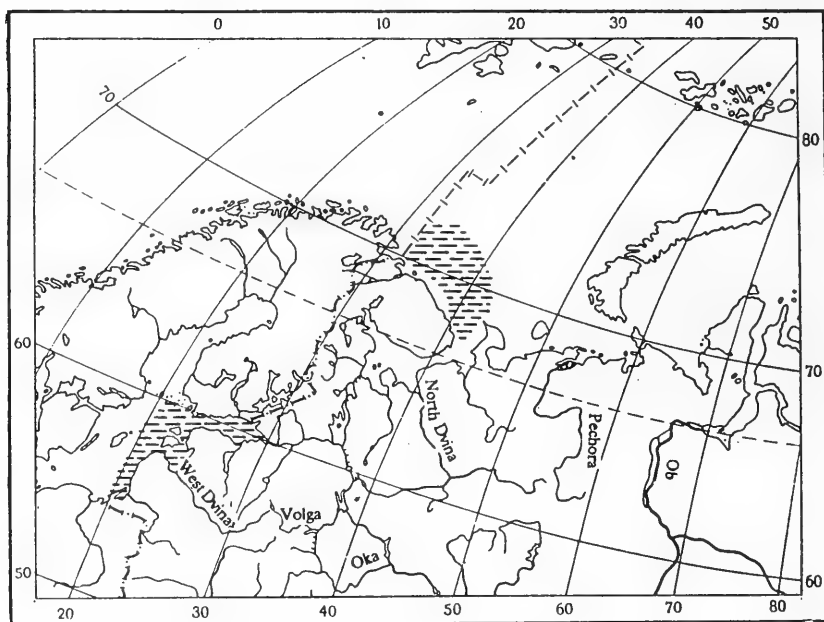
Barents Sea, Murman coast, and waters of Rybachii Peninsula; Baltic Sea, including the gulfs of Finland and Riga (Fig. 276).



493 Fig. 274. White-beaked dolphin, *Lagenorhynchus albirostris* (figure by N.N. Kondakov).



493 Fig. 275. Skull of the white-beaked dolphin, *Lagenorhynchus albirostris* (figure by N.N. Kondakov).



194 Fig. 276. Range of the white-beaked dolphin, *Lagenorhynchus albirostris*, in the USSR (V.A. Arsen'ev).

Geographic Range outside the USSR

Along the American coast, it is encountered in Davis Strait, waters of western and southern Greenland and Labrador in the north to Massachusetts Bay in the south. In the eastern part of the Atlantic, from the Barents Sea, Iceland, and Greenland to the coasts of France (Vannes),
 495 Great Britain, and Ireland. Waters of Denmark and southern Sweden in the Baltic Sea (Fig. 277). Often seen in the western waters of the Baltic Sea. (V.A.)

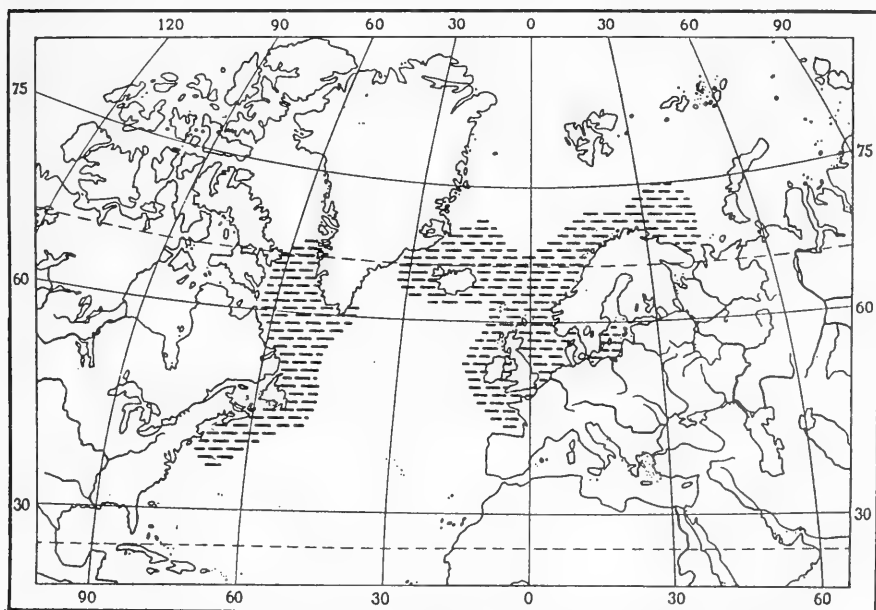
Geographic Variation

Not known.

Biology

Large herds of thousands of animals are seen in the summer months in the northern parts of the range (Barents Sea, waters of Iceland, southern Greenland, and coasts of Labrador and Newfoundland).

This species feeds mainly on benthic and bottom-dwelling fish and other animals. The stomach of examined dolphins contained cod, capelin,



494 Fig. 277. Species range of the white-beaked dolphin, *Lagenorhynchus albirostris* (V.A. Arsen'ev).

navaga, whiting, herring, and less frequently hermit crabs, cephalopods, and some mollusks.

In summer they usually live in pairs or small groups but sometimes form schools of significant strength. They probably perform regular migrations since, for example, they are encountered only in spring and summer but disappear in autumn in Davis Strait; they are more numerous in summer than winter in the waters of Norway and Great Britain. Instances of beached dolphins have been reported, although comparatively not often, on the coasts of Orkney Islands, Ireland, Sweden, Denmark, Holland, the Federal Republic of Germany, and France.

The period of mating is somewhat extended but is confined to the summer months. Most females give birth in midsummer. The embryos measured were 113 to 122 cm long but a female 305 cm long contained an embryo 165 cm long. Yet a suckling calf found on the beach was only 122 cm long.

Two species of nematodes are known among the endoparasites. *Anisakis* (*Anisakis*) *simplex* Rudolphi, wide-ranging among marine mammals, was detected in the gullet, stomach, and intestine of the white-beaked dolphin. It has also been recorded in 10 other species of toothed whales, two species of baleen whales, and Steller's sea lion in the North Sea and in the waters of the Pacific Ocean. *Halocercus lagenorhynchi* Baylis and Daubney is a parasite of the lungs (bronchi) of the white-beaked dolphin and the bottlenose dolphin; it has been detected in dolphins of the European waters of the Atlantic Ocean and in the waters of Australia (Delamure, 1955).

The white-beaked dolphin is regularly hunted on the Norwegian coasts but the volume of hunting is minimal. Previously hunting was relatively rewarding in Davis Strait but not at present, while the catch on the coasts of Great Britain is incidental. Hence this species is of very little economic importance. (V.A.)

PACIFIC WHITE-SIDED DOLPHIN

Lagenorhynchus (*Lagenorhynchus*) *obliquidens* Gill, 1865

1865. *Lagenorhynchus obliquidens*. Gill. Proc. Ac. Sc. Philadelphia, 17, p. 177. Near San Francisco, California.
1955. *Lagenorhynchus ognevi*. Sleptsov (Slepzov). Tr. Instituta Okeanologii AN SSSR, 18, p. 60, 15-20 km east of Kunashir Island, Kuril range. (V.H.)

Diagnosis

Body length up to 230 cm. The body is blackish on top and white underneath, the flanks grayish with a dark field in the middle. The premaxillae are rounded and their outer edge slightly sinuate. The temporal fossa is large, rounded. The pterygoid bones are often separated. Teeth $\frac{27-34}{28-32}$. Vertebrae 74. (V.S.)

496

Description

Body coloration is subject to considerable individual variation. Usually the upper side of the body, end of the snout, anterior portion of the dorsal fin, and the flippers are dark-colored. The flanks are lighter in color. A narrow black band runs on each side from the base of the flippers anteriorly and upward toward the corner of the mouth and posteriorly along the body up to the lower caudal stem (Fig. 278). Sometimes two symmetrical longitudinal narrow white bands run along the dorsum, commencing along the flanks near the blowhole. These bands later run onto the flanks anterior to the dorsal fin and continue up to the caudal stem.

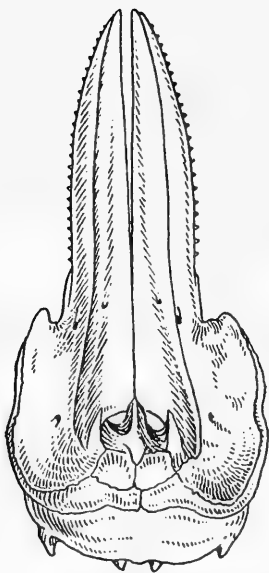
The integument is characterized by a thin dermal layer with abundant elastin fibers which are found in small bundles at the border of the subcutaneous fatty tissue and subcutaneous musculature. The embryos have whiskers on the snout.

The length of the rostrum of the skull (Fig. 279) is roughly equal to or slightly more than the length of the cranial section. The usual dental formula is $\frac{30-32}{29-31}$. The diameter of the largest tooth does not exceed



496

Fig. 278. Pacific white-sided dolphin, *Lagenorhynchus obliquidens* (figure by N.N. Kondakov).



496 Fig. 279. Skull of the Pacific white-sided dolphin, *Lagenorhynchus obliquidens* (figure by N.N. Kondakov).

5 mm. Cervical vertebrae 7, thoracic 13-14, lumbar 20-24, and caudal 30-34. Phalangeal formula: I_{1-2} , II_{6-8} , III_6 , IV_{2-3} , and V_{1-2} .

The main body measurements of the Pacific white-sided dolphin (Wilke, Taniwaki, and Kuroda, 1953) averaged for four females and ten males are respectively (in cm): body length 172 and 167; distance from tip of snout to dorsal fin 112 and 106, to anterior margin of base of flippers 43 and 42; distance from anus to caudal bifurcation 50 and 49; maximum width of caudal flukes 50 and 44; height of dorsal fin 20 and 18; length of flippers 30 and 28 and maximum width 11 and 10. The length of the largest male was 222.6 cm and of the female 221 cm.

Females weigh 67-93 kg, average 80 kg, and males 58-84 kg, average 66 kg (Japanese Hunting; Wilke, Taniwaki, and Kuroda, 1953).

The average skull dimensions (Tomilin, 1957) are (in cm): condylobasal length 40 (ten measurements), length of rostrum 22 (eight), width of rostrum at base 10 (eight), zygomatic width 20 (six), length of lower jaw 34 (eight), and length of mandibular symphysis 4 (five). (V.S.)

Geographic Distribution

North Pacific Ocean.

Geographic Range in the USSR

Coasts of the Sea of Japan, including Peter the Great Gulf and Amur and Vityaz' Bay. Waters of Kuril Islands—Shikotan, Iturup, Urup, Kunashir, and Paramushir on the Pacific Ocean as well as the Sea of Okhotsk side (Fig. 280).

Geographic Range outside the USSR (Fig. 281)

Coastal waters of Honshu and Hokkaido Islands, Pacific Ocean coast of North America from the Gulf of California (Mexico) to the Gulf of Alaska and the Aleutian Islands. (V.A.)

Geographic Variation

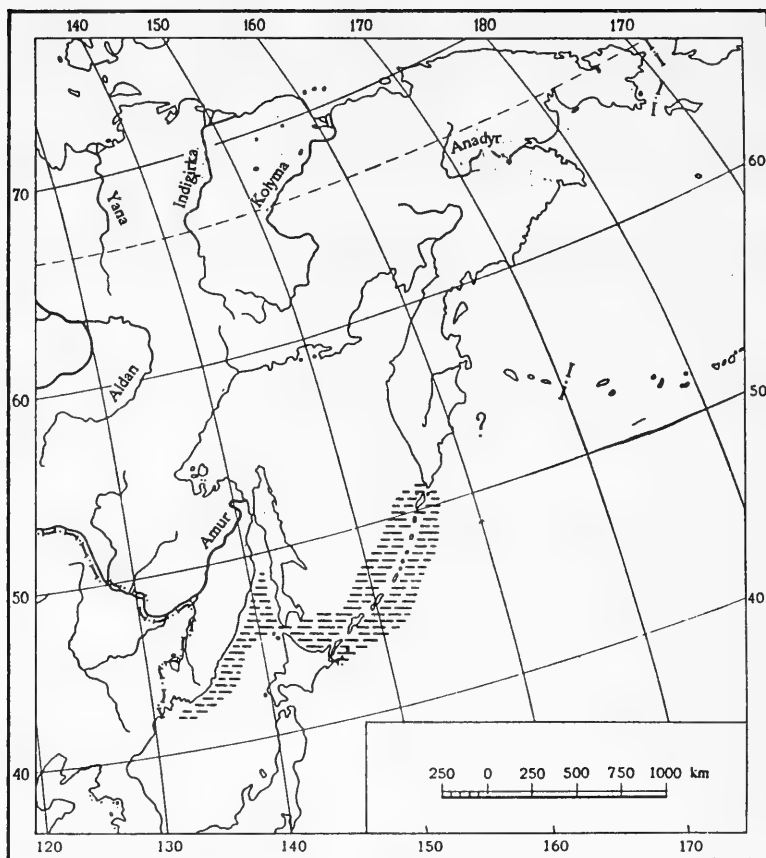
Not studied.

Biology

Population. One of the abundant species of Pacific dolphins. In some parts of the range, it sometimes forms schools of thousands of animals. It is numerous among our Kuril Islands on the Sea of Okhotsk as well as the Pacific side.

499 *Food.* Small fish and cephalopods which form large concentrations serve as the main food. Lantern fishes—Scopelidae (Myctophidae)—are of utmost importance and represent 77% of the total intake by volume, Japanese anchovy (*Engraulis japonica*) 9%, Pacific mackerel (*Scomber japonicus*) 7%, and squids ("beaks" and eye lenses probably of *Watasenia scintillans*) also 7% (Wilke, Taniwaki, and Kuroda, 1953). In the coastal waters of North America, the stomach of dolphins contained herring, salmon, sardine (*Sardinops caerulea*), saury, northern anchovy (*Engraulis mordax*), scad (*Decapterus paliaspis*), squids including *Loligo opalescens*, and jellyfish. In Nemuro Strait, the stomach of a female contained squids (*Ommatostrephes sloanei-pacificus*) and scad [Japanese horse mackerel] (*Trachurus japonicus*) (Scheffer and Slipp, 1948).

Lantern fishes are of major importance in the food intake of these dolphins in the waters of Japan. Squids were found in almost every stomach dissected but in small quantities. But their importance is undoubtedly far greater than revealed by analysis based on the volume ratio in the intake since the stomach contents contained only the remnants of squids, such as "beaks" and eye lenses (100 to 200 "beaks" in one stomach). Apparently the small schooling fish and squids constitute the main food of dolphins in this region.



497 Fig. 280. Range of the Pacific white-sided dolphin, *Lagenorhynchus obliquidens*, in the USSR (V.A. Arsen'ev).

Daily activity and behavior. These dolphins are usually more active in the day. They are encountered in small groups as well as in large herds. Herds comprising animals of different ages predominate in the summer months but sometimes separate groups of young dolphins are also encountered.

These dolphins are more often seen in large bays and gulfs than in the open sea. They quite often follow a ship but on closing in on it, dive to a depth of 1-3 m. Sometimes playful dolphins leaping high above the water land on their side or back with a loud thud and raise

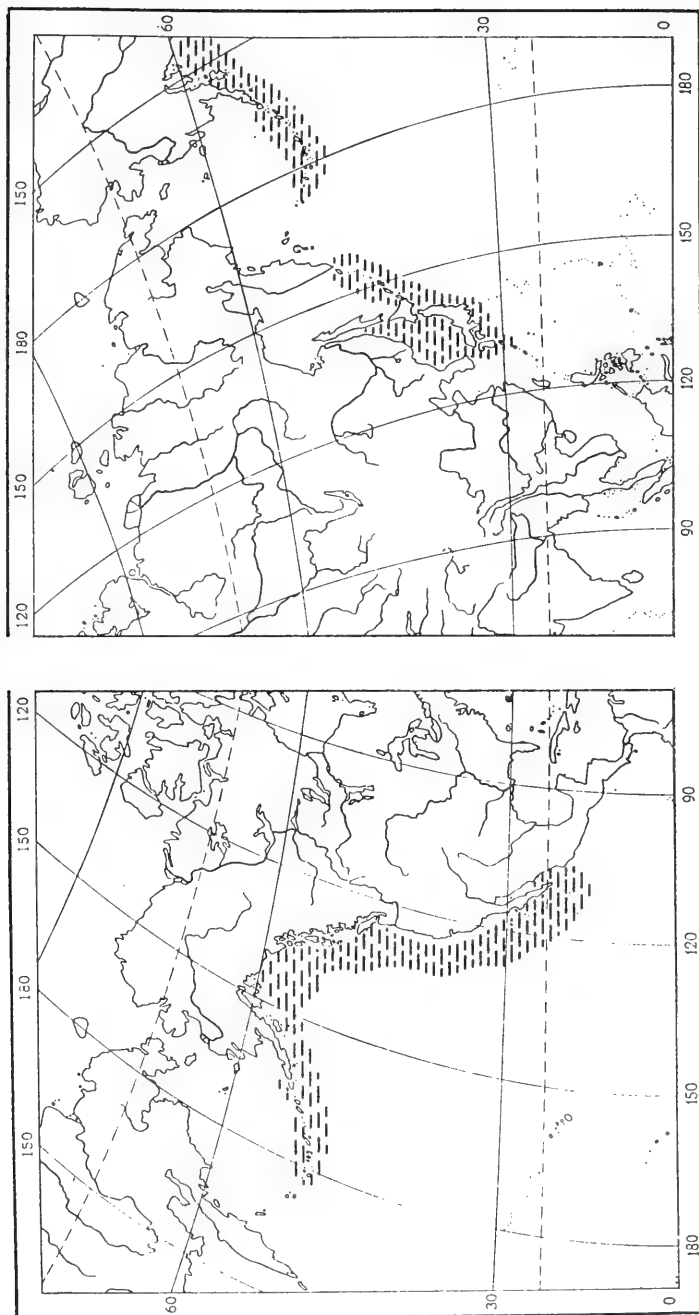
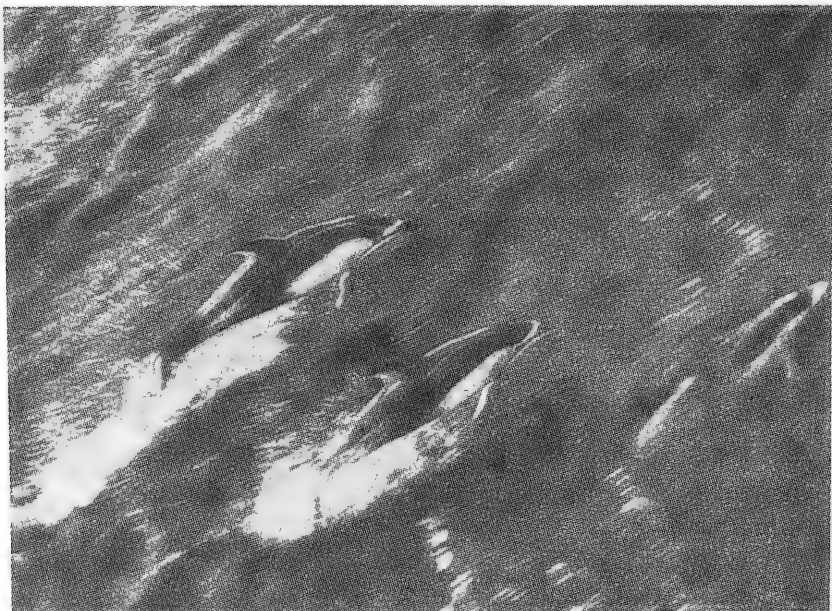


Fig. 281. Species range of the Pacific white-sided dolphin, *Lagenorhynchus obliquidens* (V.A. Arsen'ev).

much spray (Fig. 282). These dolphins are encountered in groups with
500 other species also. On one occasion an adult dolphin trying to rescue a
harpooned comrade was observed. It dove frequently between the ship
and the injured dolphin and each time pushed it farther away from the
ship. These animals survive well in tanks, live long, and can be trained
well. They quickly learn to play with a ball, jump through a hoop, etc.,
and to snatch food from the trainer's hand (Tomilin, 1962).

Migration. Seasonal migrations probably do occur but the information available is highly fragmentary. In the waters of California, these dolphins are noticed in the winter months (November, December, February, March, and April); on the coasts of Washington state in March and later in July, August, September, and November; on the coast of British Columbia in July; and in the waters of the Alaskan peninsula from July to September.

Judging from the Japanese hunting experience, these dolphins are encountered in early March on the Pacific Ocean coasts of Honshu at 36° N lat. and in mid-March at 39 to 40° N lat. where they remain until June, partly advancing farther north toward Hokkaido coasts. In summer and autumn, large schools are seen in the coastal waters of the



Kuril Islands in the Pacific Ocean and in the Sea of Okhotsk. A large school was found on August 1, 1951, feeding on anchovy in the region of Chetvertyi Kuril Strait; at the end of August, a herd more than 1,000 strong was sighted on the Pacific Ocean side of Iturup Island where saury concentrations were present. At the end of September, a large herd of these dolphins was noticed southeast of Shikotan Island where, too, a school of saury was encountered. Hunting on a small scale is resumed in the autumn months on the coasts of Japan (Klumov, 1959).

Reproduction, growth, and development. Mating and parturition occur in summer. An embryo 22 mm long, detected in September, had grown to 370 mm by December and 761 mm by March. A male 124 cm long turned out to be a suckling calf (weight 29.5 kg). The ovaries of a 171-cm long female (weight 62 kg) did not contain corpora lutea but the Graafian follicles were well developed; this female was close to attaining sexual maturity (Houck, 1961). Females 180 cm or longer were already with embryos. In oceanariums, mating of female white-sided dolphins with male bottlenose dolphins has been observed time and again (Tomilin, 1962).

The parasites of these dolphins have not been studied. (V.A.)

Economic Importance

These dolphins are regularly hunted along with other species only in the waters of Japan. Their annual catch does not exceed 1,000 head. The weight of the females varies from 67-93 kg (mean 80 kg) and of males from 58-84 kg (66 kg). They are of little economic importance.

Hunting is carried out using the same small ships (20 to 30 tons) and the very same methods as practiced in hunting other species of dolphins. The dorsal fin, flippers, and caudal flukes are first separated from the trunk of the killed animal. The skin is then peeled off in two layers together with the subcutaneous fat and the flesh is separated in large chunks from the vertebral column. The intestine, heart, and other internal organs are then cut out and the ribs chopped. The flesh, heart, lungs, and liver are used as food. The skin is tanned to make low-quality leather goods. The blubber is melted into oil; the blubber from the head and in the hollow of the jaws can be converted into a high-grade machine oil. The skeletal bones as well as all the remnants are used for making fertilizer meal (Wilke, Taniwaki, and Kuroda, 1953; Siebenaler and Caldwell, 1956; Klumov, 1959; Tomilin, 1962).

Large schools of these white-sided dolphins prevailing in the waters of the Kuril Islands suggest the possibility of their organized hunting here. (V.A.)

BROADSNOUT DOLPHIN

Lagenorhynchus (Peponocephala) electra Gray, 1846

1846. *Lagenorhynchus electra*. Gray. Zoology. Voyage Erebus and Terror, 1, p. 35. Type locality not established.

1848. *Delphius pectoralis*. Peale. U.S. Explor. Exped., 8, p. 32. Hawaiian Islands.

1868. *Electra obtusa*. Gray. Synopsis Whales Dolphins. Brit. Mus., 7. Substituted for *Lagenorhynchus electra* Gray, 1846. (V.H.)

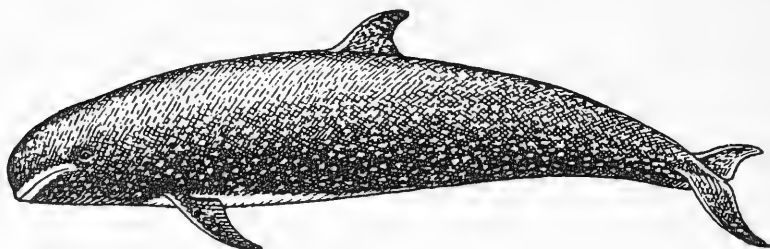
The broadsnout dolphin differs significantly from all other species of the genus *Lagenorhynchus* in several characteristics: it has no beak whatsoever or such is barely visible and not demarcated from the forehead; a uniform arcuate line of the profile is formed from the blowhole to the edge of the mouth. The preorbital depression is larger than in the other species of the genus. The first three vertebrae, and not the first two as in the other species, are fused. The general body shape is more elongated, with a relatively longer caudal stem. The color is monochromatic, dark, without black, gray, or white fields; a light-colored (white) field is seen only in the cervical zone and on the breast; sometimes, a similar field is seen in the posterior section of the abdomen (Fig. 283).

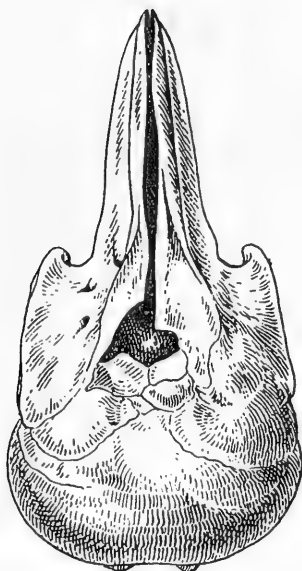
This is a somewhat peripheral form of the genus and reveals features of similarity and association with the genera *Pseudorca* (false killer whale) and *Feresa* (dwarf killer whale). (V.H.)

Its range is known only from some fragmentary information.

Its presence has not been established in USSR waters but residence in or transgressions into the Sea of Japan and waters of the Kuril Islands are possible.

Outside the USSR, it is found in tropical seas up to north of 10° N lat. Its presence has been indicated in the waters of Senegal, the Gulf of Guinea, India, Indonesia, Hawaiian Islands, and Japan (transgression





501 Fig. 284. Skull of the broadsnout dolphin, *Lagenorhynchus (Peponocephala) electra* (figure by N.N. Kondakov).

of a herd of 500 animals in 1965 into Suruga Bay on the ocean side of Honshu; Nishiwaki and Norris, 1967). (V.H.)

Biology is almost not known. Very rare. In January, 1963, fourteen dolphins were caught in a net in one of the bays on the Pacific Ocean side of Honshu Island. All of them showed their heads above the water most of the time, thus exhibiting near-total fearlessness of man. Held in an oceanarium they exhibited no restlessness and were at peace with man (Nishiwaki, 1965). (V.A.)

Genus of False Killer Whales

Genus *Pseudorca* Reinhardt, 1862

1846. *Phocaena crassidens*. Owen. Hist. Brit. Foss. Mamm. p. 516.

1862. *Pseudorca*. Reinhardt. Overs. Danske Vidensk. Selsk. Forh., p. 151. (V.H.)

Medium-size dolphins, with body length up to 6 m.

The body is elongated. The small rounded head has a fairly large adipose body [melon]. The obtuse "beak" is barely perceptible. The upper jaws are slightly longer than the lower. The relatively small dorsal fin

502 lies midbody and is deeply notched posteriorly. The flippers are narrow and pointed at the tip.

The body is black but the ventral side somewhat lighter.

The rostrum is short, not longer than the cranium, but broad. The premaxillae are very broad and identical throughout their length. Their anterior margin is rounded. The reduced pterygoid bones are adjacent. Teeth $\frac{8-11}{8-12}$. Vertebrae 50-51. Phalangeal formula: I_{1-2} , II_{6-8} , III_{5-6} , IV_{2-4} , and V_{1-2} . The sternum consists of four sections. Ribs 10 pairs, of which four articulate with the sternum.

False killer whales feed mainly on schooling fish and cephalopods. Mating and parturition are protracted.

These whales are distributed in the warm and temperate waters of the Pacific, Indian, and Atlantic oceans. They are not caught in USSR waters but might possibly be found along the Kuril Islands and in the Sea of Japan and the Baltic Sea.

Fossils of false killer whales have been detected in the Upper Pliocene of Europe and Japan.

The genus comprises a single species: the false killer whale, *P. crassidens* Owen, 1816. (V.S.)

FALSE KILLER WHALE

Pseudorca crassidens Owen, 1846

1846. *Phocoena crassidens*. Owen. British Fossil Mamm. and Birds, p. 516. Lincolnshire, England (subfossil specimen).

1882. *Pseudorca mediterranea*. Giglioli. Zool. Anzeiger, 5, p. 268. Mediterranean Sea. (V.H.)

Diagnosis

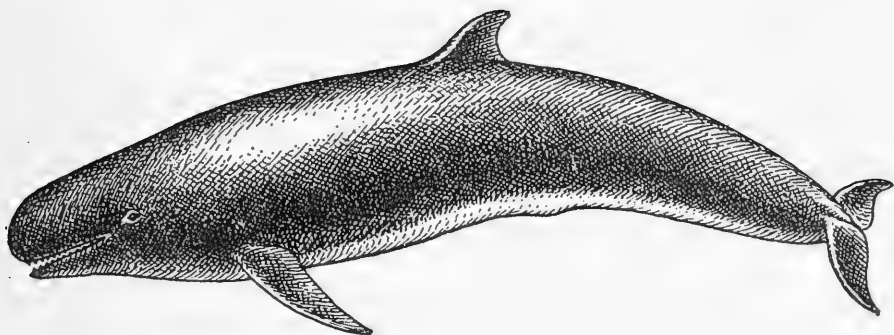
Only species of the genus.

Description

The body is elongated, spindle-shaped, and the head relatively small. It somewhat resembles the killer whale but the body build is less compact, the head more elongated, and the dorsal fin considerably shorter. The flippers are not rounded but narrow and pointed (Fig. 285).

Very light-colored star-shaped scars are often seen on the black surface of the body. A gray longitudinal band sometimes occurs on the midabdomen and in the region of the urogenital opening.

Teeth usually number $\frac{8}{10}$. Unlike those of the killer whale, their cross section is not oval but circular.



503 Fig. 285. False killer whale, *Pseudorca crassidens* (figure by N.N. Kondakov).

The width of the rostrum increases with age and can be correlated with the intense growth of the adipose body [melon]. Cervical vertebrae 7, thoracic 10, lumbar 9-11, and caudal 22-24. The anterior and sometimes all the cervical vertebrae are fused.

The indices of the main body measurements of the false killer whales as percentage of the total length of males (three specimens) with a body length of 279-465 cm and females (two) with a body length of 251 and 267 cm (Tomilin, 1957) are respectively: distance from tip of snout to blowhole 9.6-12.4 and 11.7-12.3, up to base of flippers 14.5-19.6 and 15.3-21.4, up to posterior margin of dorsal fin 51.2-62.0 and 63.2-71.7; length of base of dorsal fin 15.2-15.7 and 13.8-14.7, height of dorsal fin 8.3-8.6 and 7.4-8.3; length of flippers 11.8-13.2 and 11.5-12.6, maximum width of flippers 4.7-5.0 and 4.6-5.0; width of caudal flukes (from tip to tip) 24.0-24.4 and 20.9-21.4. The largest of the false killer whales caught measured 596 cm in length. Males are 0.6-1.0 m longer than females. False killer whales weigh up to 1.5 tons.

The main dimensions of the skull (eight measurements) of adult false killer whales (Tomilin, 1957) are (in cm): condylobasal length 54-62, length of rostrum 27-30, width of rostrum at base 18-21, and length of lower jaw 46-51 (Fig. 286).

The vertebral sections constitute (as percentage of length of the vertebral column): cervical 3, thoracic 17, lumbar 31, and caudal 49 (Slijper, 1936). (V.S.)

Geographic Distribution

Encountered in temperate and warm waters of the Northern and Southern hemispheres (Fig. 287).

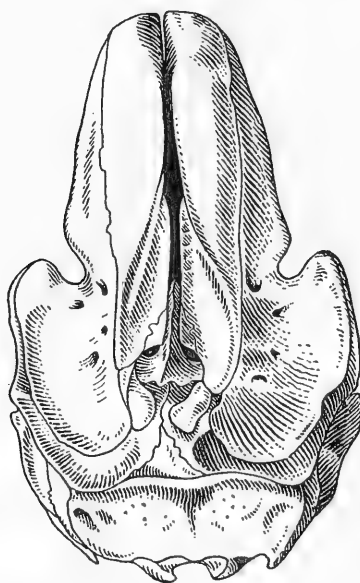
Geographic Range in the USSR

Waters of the Kuril Islands (apparently the southern islands) and probably the Sea of Japan. Transgressions into our waters of the Baltic Sea are quite possible.

Geographic Range outside the USSR

Encountered in the Atlantic Ocean everywhere from the North Sea and North Carolina⁸ to the South African and South American coasts (Tierra del Fuego). It has been reported on the eastern (Baltic) coasts of Denmark, western and partly eastern (evidently the southernmost) coasts of Sweden, and on the Baltic coasts of the Federal Republic of Germany (Kiel Bay). Not reported on the coasts of Poland.

It has been reported in the Pacific Ocean from Washington state in the north to the coasts of Peru, probably Chile, New Zealand, Australia,



503 Fig. 286. Skull of the false killer whale, *Pseudorca crassidens* (figure by N.N. Kondakov).

⁸ References to habitation farther north (Davis Strait and Aleutian Islands; Tomilin, 1957, 1962) have either not been confirmed (Murie, 1959; Hall and Kelson, 1959; Manvill and Joung, 1965), or have been questioned, or treated as erroneous (Herskovitz, 1966). (V.H.)

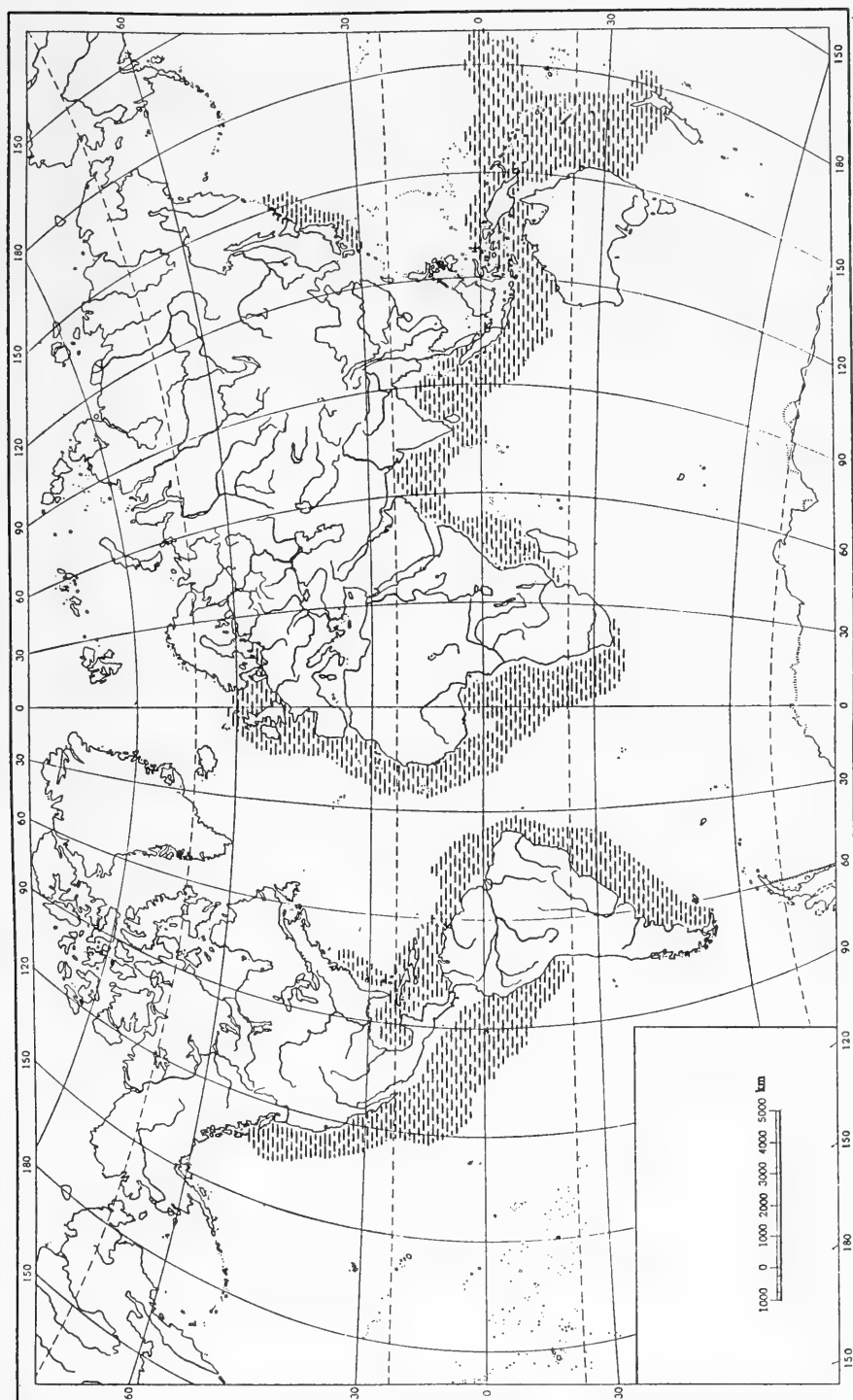


Fig. 287. Species range of the false killer whale, *Pseudorca crassidens* (V.A. Arsen'ev).

and Tasmania in the south; it has been reported in the Indian Ocean in the warm and temperate water zones.

505 Numerous beached animals have been found on the coasts of Great Britain, Denmark, Holland, the Baltic and Mediterranean seas in the eastern part of the North Atlantic; in the western part, on the coasts of North Carolina and Florida states, Cuba, Venezuela, Brazil, and Argentina. In the Pacific Ocean, beached animals have been found on the Kuril Islands, the coasts of Japan, Galapagos Islands, California, and Mexico; and in the Indian Ocean, on the coasts of Sri Lanka, India, South Africa, and Australia (Tomilin, 1962; Mitchell, 1965; Fiscus and Niggol, 1965; Nishiwaki, 1966). (V.A.)

Geographic Variation

Not established.

Biology

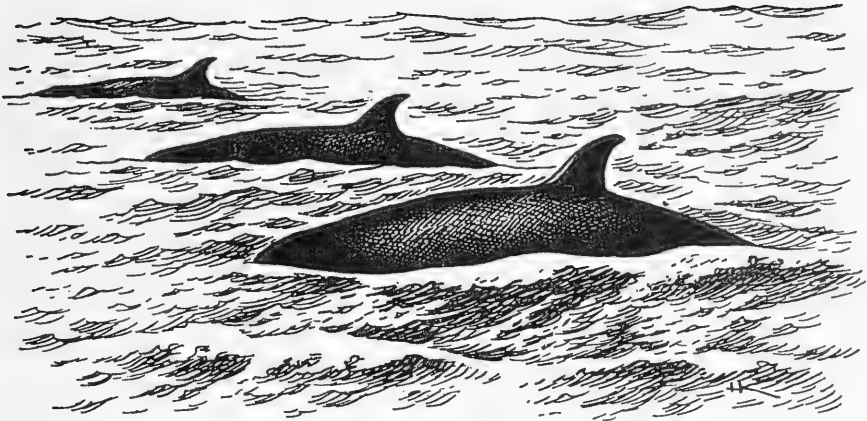
As the range of the false killer whale is very large and instances of beaching (sometimes in large herds) are well known, this species could correctly be classed as a relatively abundant one.

Food. Fish (e.g., haddock, cod, and salmon) and some species of cephalopods serve as the food of the false killer whale; these animals quite often come close to the coast in pursuit of food objects. It is at such times that they become stranded on the shoals.

Behavior. False killer whales more often live far from the coasts in the open sea in small groups although sometimes they do form large herds (Fig. 288). Instances of large herds of these dolphins being cast on the beach are known. For example, in Mar del Plata in Buenos Aires province of Argentina, 835 false killer whales were stranded on a sandy beach on October 10, 1946 and perished soon thereafter. They suffered from extreme fatigue and had slowly sunk into the sand (Obruchev, 1949).

Migrations of false killer whales have not been studied.

Reproduction. Judging from the fact that embryos of different sizes are encountered simultaneously, mating and parturition are undoubtedly protracted among these dolphins. An embryo 117 cm long was well pigmented while another embryo 160 cm long was almost mature. The largest of the embryos examined was 183 cm long. It has been reckoned that females attain sexual maturity at a body length of 366 to
506 427 cm. An examination of many groups of false killer whales that perished through beaching established a male:female ratio of almost one in each herd.



505

Fig. 288. False killer whales at sea (figure by N.N. Kondakov).

Enemies, diseases, parasites, mortality, and competitors. Skin parasites have not been reported but two species of helminths have. The nematode *Anisakis (Anisakis) simplex* Rudolphi, parasitizing the gullet, stomach, and intestine, has been found in ten other species of toothed whales, two species of baleen whales, and in Steller's sea lion, as well as in the false killer whale. It has also been detected in various species of marine mammals in the North Sea, on the coasts of Kamchatka, Japan, and New Zealand. The acanthocephalan *Bolbosoma capitatum* Linstow parasitizes the intestine of the false killer whale, the pilot whale, and the sperm whale in the Atlantic Ocean and the Mediterranean Sea. (V.A.)

Economic Importance

There is no special hunting for the false killer whale; it is caught incidentally while hunting for other species. In some cases, the carcasses of beached animals are utilized. The overall weight of a false killer whale may reach 1.5 tons (Delamure, 1955; Sleptsov, 1955; Tomilin, 1957, 1962). (V.A.)

Genus of Killer Whales

Genus *Orcinus* Fitzinger, 1860

1846. *Orca*. Gray. Zoology. Voyage Erebus and Terror, I, p. 33. *Orca gladiator* Gray = *Delphinus orca* Linnaeus, 1758. Nom. praeocc.
—*Orca* Wagler, 1830 = *Hyperoodon* Lacépède.
1860. *Orcinus*. Fitzinger. Wiss. Popul. Naturg. Säugeth., 6, p. 204.

1870. *Gladiator*. Gray. Proc. Zool. Soc. London, p. 71. *Delphinus orca* Linnaeus, 1758.

1933.⁹ *Grampus*. Iredale and Troughton. Rec. Austr. Mus., 19 (1), p. 28. *Delphinus orca* Linnaeus, 1758. (V.H.)

Dolphins of large proportions, being the largest members of the family. Body length up to 10 m.

The head is somewhat flattened dorsoventrally. There is no "beak". The broad flippers are oval in shape. The dorsal fin is very high, especially among males (up to 1.7 m). The overall color of the body along the upper side and flanks is black while the belly and neck are white. A white patch occurs on each side posterior to the dorsal fin and on the temple above the eye (sometimes these patches are lacking).

The broad and flattened rostrum is slightly shorter or as long as the cranium. The maxillae are well developed and very broad. The occipital crest is absent in the young but high among the adults, especially males. The temporal fossa is large. The teeth are large, number $\frac{10-14}{8-14}$, compressed front to back and have extremely well-developed roots. Vertebrae 50-52. The sternum consists of three or four sections.¹⁰ The length of the phalanges of the digits and the metacarpals is less than their width. Phalangeal formula: I_2 , II_{6-7} , III_{4-5} , IV_{3-4} , and V_{2-3} .

507 The killer whale is sarcophagous and attacks even large whales. The periods of mating and parturition are protracted. Gestation probably requires one year.

These whales are distributed in the World Ocean except in glacial regions of the Arctic and the Antarctic.

Fossil remains have been detected in the Middle Pliocene of Europe.

The genus comprises a single species: the killer whale *O. orca* Linnaeus, 1758.

There is no special hunting of the killer whale. (V.S.)

KILLER WHALE

Orcinus orca Linnaeus, 1758

1758. *Delphinus orca*. Linnaeus. Syst. Nat., ed. X, I, 77. Eastern part of the northern half of the Atlantic Ocean ("Oceano Europaeo").

⁹ The introduction of the name *Grampus* to denote the genus of killer whales is associated with so many inaccuracies that it must be considered irrational from the viewpoint of nomenclature. Yet the name (*Grampus orca*) did prevail in the literature for sometime. Today, as earlier, it is used only in reference to Risso's dolphin (*Grampus griseus*). (V.H.)

¹⁰ According to other data, the sternum is not segmented (Sleptsov, 1955).

1789. *Delphinus gladiator*. Bonnaterre. Tabl. Encycl. Méth. Cétologie, p. 23. Spitsbergen, Davis Strait, New England.
1869. *Orca ater*. Cope. Proc. Ac. Nat. Hist. Philadelphia, 21, p. 22. Northern Pacific Ocean ("Northwestern coasts from Oregon to Aleutian Islands").
1869. *Orca rectipinna*. Cope. *Ibid.*, 21, p. 22. Californian coast.
1874. *Orca ater* var. *fusca*. Dall. In: Scammon. Marine Mammals of the N. W. coast of N. America, p. 298. Coasts of California and Oregon. (V.H.)

Diagnosis

Only species of the genus.

Description

This whale has a strongly built body, a fairly large head, a large mouth, and is a powerful predator. Large rounded flippers (Fig. 289) are a characteristic feature. Another distinctive feature of this whale is the high dorsal fin, which is straight along the posterior margin.

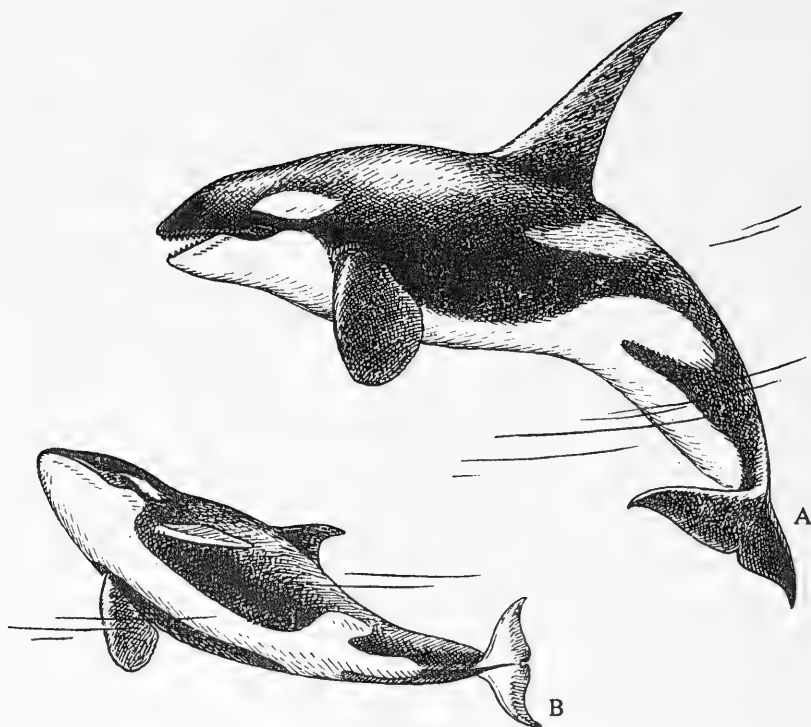
This whale exhibits distinct sexual dimorphism in the dimensions of the dorsal fin, which is considerably larger in the males. The size and relative dimensions of the flippers in both sexes and the caudal flukes among males increase with age. Unlike in other whales, the head in the killer whale (Fig. 290) becomes relatively shorter with advancing age while the caudal section becomes elongated, i.e., the elongation of the head is relatively less compared to the caudal section (Ivanova, 1959).

The white coloration on the belly is divided posteriorly into three tongues, of which the two lateral ones (right and left) terminate behind the anal opening while the middle one may terminate at the same point or run along the right up to the caudal flukes (which then merge with the white coloration), or be altogether absent. Sometimes the right and left white tongues fuse posterior to the dorsal fin. Wholly dark-colored killer whales with only a white spot under the eye are encountered in the Far East.

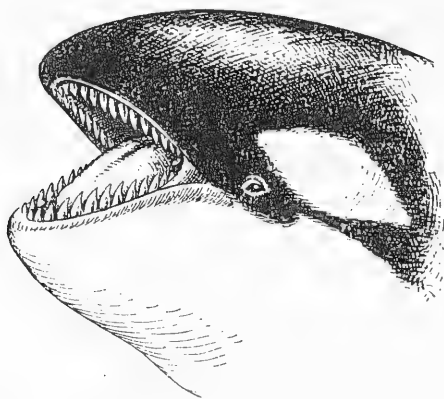
Unlike most other dolphins, the integument is characterized by a well-developed dermal layer with a dense network of fascicles of collagen fibers. Small processes project into the dermal papillae from the epidermal septa. Up to seven hairs are seen on the upper jaw of embryos.

Sex- and age-related variations are distinctly seen in the skull. The temporal fossa and occipital crest enlarge with age. Among adult males, indices of the width of the rostrum are slightly higher than in the young.

508 The lower jaw in males is relatively longer than in females. The occipital crest of adult males is larger than that of females.



508 Fig. 289. Killer whale, *Orcinus orca* (figure by N.N. Kondakov), A—male; B—female.



508 Fig. 290. Head of the killer whale, *Orcinus orca* (figure by N.N. Kondakov).

The teeth are covered with enamel and are very strong. When the mouth is closed, the teeth on the upper jaw fall in the gaps between the lower teeth, thus forming a powerful gripping apparatus. The teeth of the killer whale, compressed front to back, have apparently adapted to feeding on large quarry from which the killer whale can tear off large chunks of flesh. The foreteeth, inclined slightly forward and outward, are capable of withstanding extremely powerful jerks of the quarry while the middle and hind teeth perform the function of holding it firmly (Tomilin, 1957). The surface of the teeth is sometimes worn down to the pulp cavity. Vertebrae: cervical 7, thoracic 11-12, lumbar 10, and caudal 21-24. The first two to three vertebrae are usually fused. The percentages of the different sections of the vertebral column to its total length constitute: cervical 3.2, thoracic 22.9, lumbar 28.0, and caudal 45.9. Ribs 11-12 pairs, of which 5-7 anterior pairs articulate with the third or fourth section of the sternum (Tomilin, 1957).

The maximum length of 320 male killer whales caught in the waters of Japan during 1948 through 1957 was 9.4 m, of 247 females 8.2 m. 509 Among these killer whales, males with a body length of 6.3 m and females 6.0 were more common. Males of maximum proportions attain a body length of 10 m and females 8.2 m (Nishiwaki and Handa, 1958).

The main body dimensions of males (based on measurements of two to four animals) and females (one to three animals) vary as follows (in cm): body length 579-830 and 495-670; distance from tip of snout to commencement of dorsal fin 245-400 and 335, up to blowhole 80-90 and 75, up to anal opening 221-273 and 225; length of base of dorsal fin 77-91 and 62, height of dorsal fin 121-170 and 52-95; and width of caudal flukes 195-279 and 99-139.

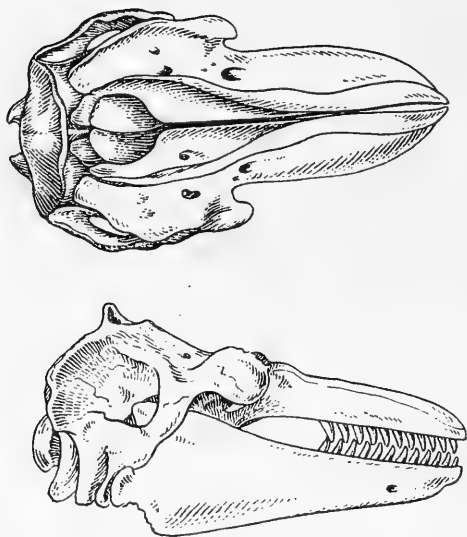
The main measurements of the skull (Fig. 291) of five adult males and one adult female killer whale (Tomilin, 1957) are respectively (in cm): condylobasal length 100-112 and 91, zygomatic width 68-78 and 57, length of rostrum 51-57 and 48; width of rostrum at base 34-37 and 27, and length of lower jaw 85-95 and 74. (V.S.)

Geographic Distribution

The killer whale represents a cosmopolitan species. It inhabits coastal and oceanic waters of the world's oceans, including the Arctic and Antarctic seas.

Geographic Range in the USSR

Barents Sea, northwestern and western parts of the Kara Sea (does not transgress into its eastern part nor into the Laptev Sea), coastal waters of



509

Fig. 291. Skull of the killer whale, *Orcinus orca* (figure by N.N. Kondakov).

Novaya Zemlya, Murman coast, Kil'din Island, Rybachii Peninsula, and the White Sea (Fig. 292). Transgressions into our waters of the Baltic Sea are highly possible (transgression into bay near Gdansk is known).

In the Pacific Ocean waters of the Soviet Union, this species is distributed everywhere in the seas of Japan and Okhotsk, around the Kuril Islands, in the Bering Sea, near the Commander Islands, in the Bering Strait, and in the southern part of the Chukchi Sea (probably north of 70° N lat.).

Geographic Range outside the USSR

From the coasts of Spitsbergen, Greenland, and Baffin Bay in the north to the southern waters of the Atlantic Ocean. It is quite common in much of the eastern and western halves of the Atlantic (coastal regions of Great Britain, Norway, Holland, France, western Africa, Atlantic coast of North and South America, and the Mediterranean Sea). It inhabits the westernmost, southwestern, and southern parts of the Baltic Sea up to Gdansk (Danzig), including the bay (Fig. 293).

In the Pacific Ocean, it is encountered off the coasts of the Korean peninsula, Japan, Aleutian Islands, and Alaska, including its northern half (noticed off Cape Barrow, 71° 24' N lat.), off the Pacific coast of North America and Mexico, and along the coasts of South America from Panama to Tierra del Fuego. It lives in the Indian Ocean and along

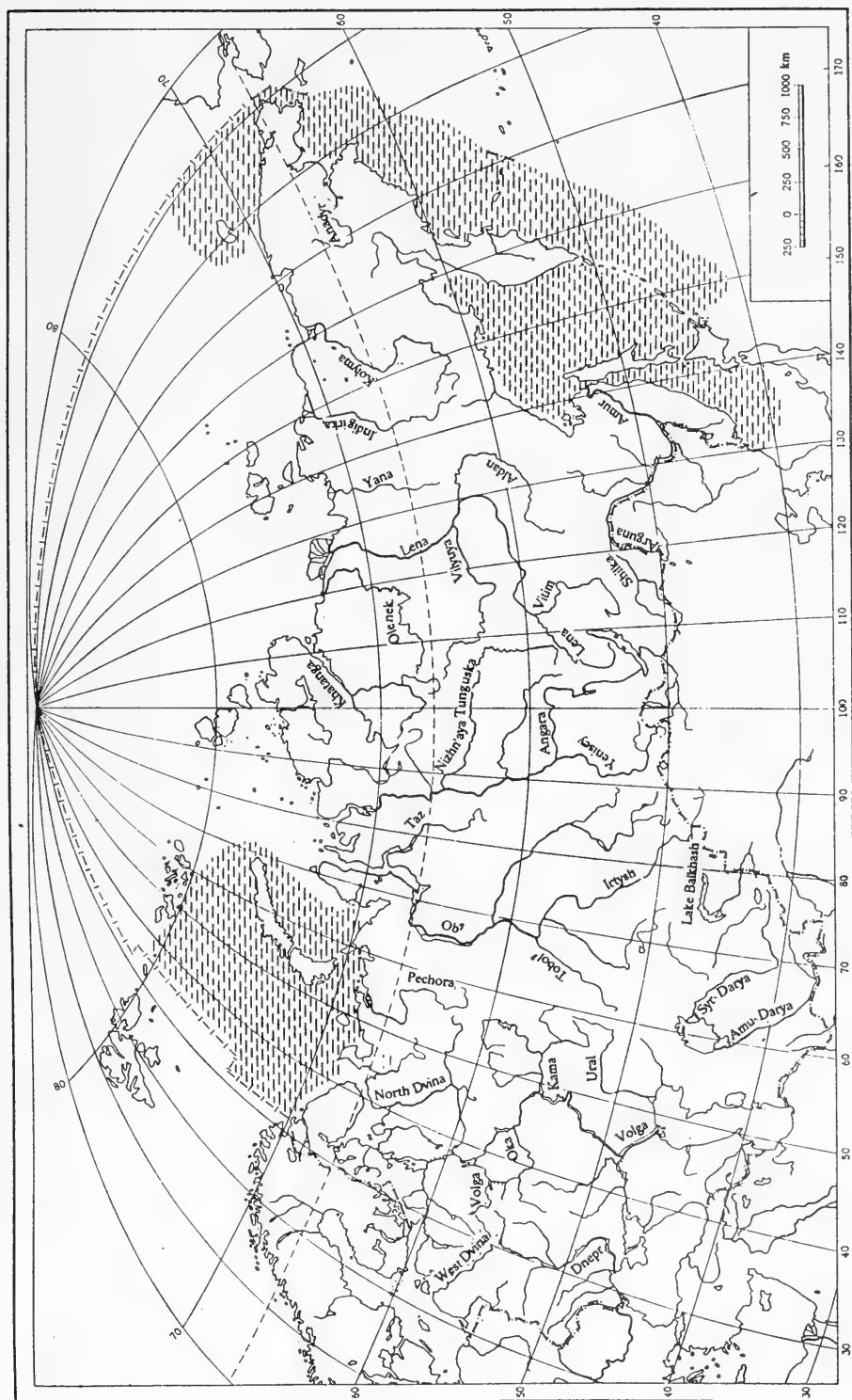


Fig. 292. Range of the killer whale, *Orcinus orca*, in the USSR (V.A. Arsen'ev).

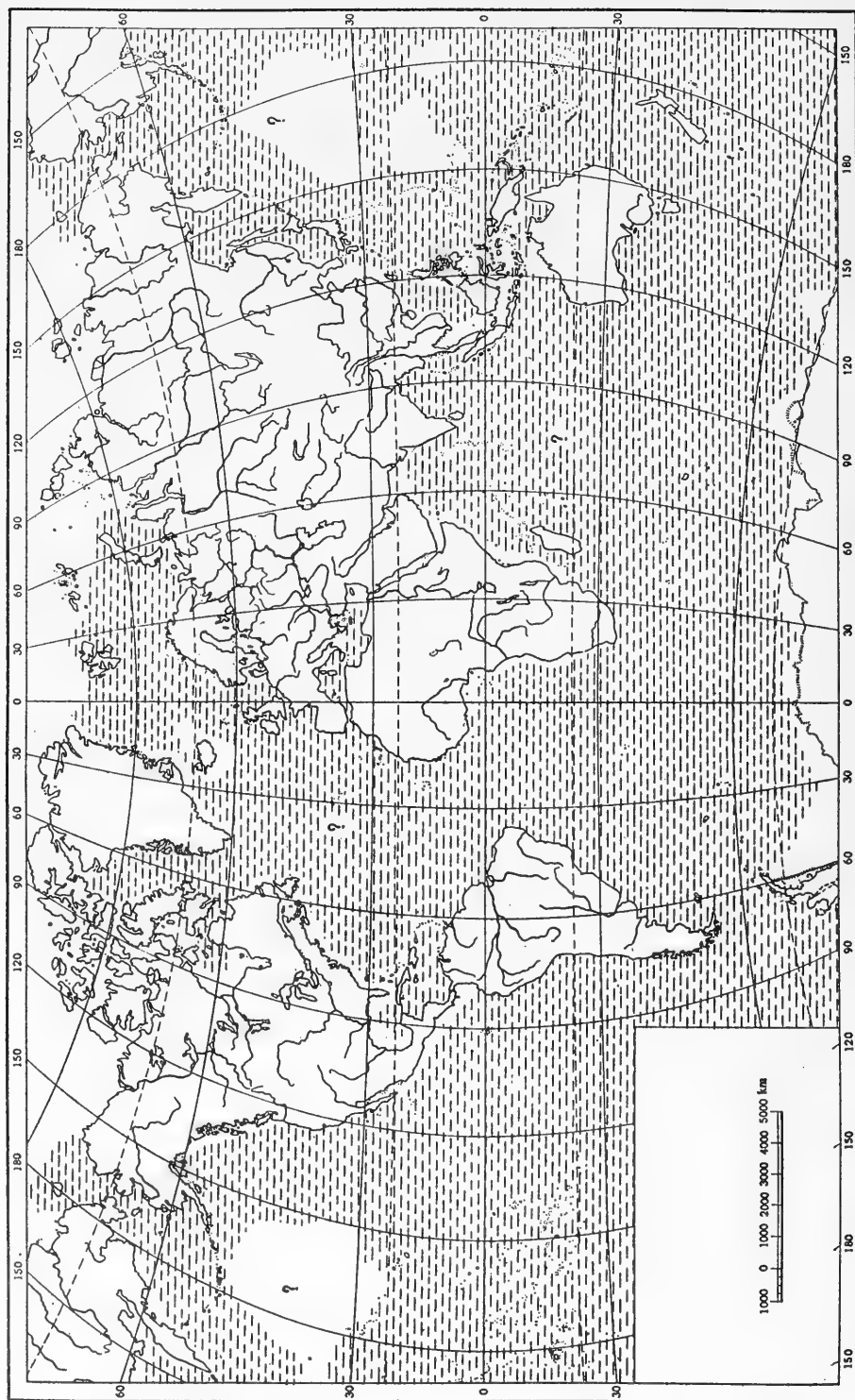


Fig. 293. Species range of the killer whale, *Orcinus orca* (V.A. Arsen'ev).

the coasts of Australia and New Zealand. It is widely distributed in the Antarctic where it reaches the high southern latitudes, right up to the zone of permanent ice. (V.A.)

Geographic Variation

In spite of the extensive distribution of this species in the World Ocean, no geographic variation has been established. Sometimes the Pacific killer whale is regarded as a species (subspecies), *Orcinus rectipinna* Cope, 1869, but the characteristics of this form have not been established, albeit mention has been made that its dorsal fin is not as high as in the Atlantic species (Hall and Kelson, 1959). (V.A.)

Biology

Population. One of the abundant species of dolphins. It is regularly encountered in the World Ocean (usually in small groups) and is fairly uniformly distributed over its immense range.

Food. The killer whale is the only true carnivore in the order of cetaceans and even consumes warm-blooded animals. Its food is quite diverse: chum salmon, chinook salmon, coho salmon, cod, capelin, halibut, skate, shark, herring, smelt, etc. Cephalopods are consumed quite often and sometimes various types of marine birds. The killer whale is known to consume seals and small dolphins and to attack fur seals, Steller's sea lion, and even walruses (an instance of a group of killer whales attacking a herd of walruses was observed from an airplane; Zenkovich, 1938b). There are frequent references in the literature to the killer whale lying in wait around the coastal rookeries of fur seals and Steller's sea lion but the many observations reported in recent years do not confirm this information (V.A. Arsen'ev). Reports of the killer whale attacking balaen whales and tearing out their tongues and large chunks of blubber, and even killing large animals, have been copied from book to book from the middle of the last century without critical review. Even a recent and thorough publication (Tomilin, 1957) describes the methods of killer whale groups attacking large whales, presenting information copied from various sources. Such reports give rise to considerable doubt.

A study of the stomach contents of several hundreds of killer whales caught in a ten-year period in the waters of Japan revealed that squids (octopuses to a very small extent) and fish (including sharks) represent the main food while marine mammals play a secondary role. The number of stomachs with remnants of dolphins was more than double the number of stomachs with remnants of seals. Among fish, cod predominated,

followed by (using the source terminology) flatfish (probably flounder, halibut, etc.). Sardines, salmon, and tuna were of lesser importance. Some stomachs revealed mackerel, greenling, sea perch, and bonito, which have no practical importance as food for the killer whale. Dolphins of three species exclusively represent the cetaceans found in the stomach remnants: Dall porpoise (*Phocoenoides dalli dalli* and *P. d. truei*) found in the stomach of killer whales on Hokkaido coasts and blue-white dolphin (*Stenella coeruleoalba*) in killer whales from the Pacific waters off Honshu. There were some finds of pilot whales, beaked whales, and two cases of sei whales (chunks of flesh). Young killer whales up to 4.3 m long feed exclusively on squids and fish. They begin attacking seals and dolphins as their body proportions increase and thus remnants of seals and dolphins are found in the stomach of only older killer whales (Nishiwaki and Handa, 1958). In July and August, 10 stomachs of killer whales were found filled with remnants of fish and squids (11 other stomachs in the same months were empty). No remnants whatsoever of marine mammals were found (Ivanova, 1961c).

In the eastern half of the North Pacific Ocean, 10 stomachs of killer whales were investigated. Of these, one was caught close to Kodiak Island in the Gulf of Alaska, five near San Francisco, and four in Californian waters. Two of these stomachs were empty while the remaining eight contained the remnants of marine mammals (California sea lion, Steller's sea lion, elephant seals, two species of dolphins, and Minke whale), halibut, ocean sunfish, shark, and squids. The frequency of encounter of the remnants of these food objects is shown below.

Quantitative characteristics of the food of
killer whales (number of finds)
(Rice, 1968)

California sea lion, <i>Zalophus californianus</i>	3
Steller's sea lion, <i>Eumetopias jubatus</i>	4
Elephant seal, <i>Mirounga angustirostris</i>	7
Harbor porpoise, <i>Phocoena phocoena</i>	2
Dall porpoise, <i>Phocoenoides dalli</i>	2
Minke whale, <i>Balaenoptera acutirostrata</i>	1
Opah, <i>Lampris regius</i>	2
Pacific halibut, <i>Hippoglossus stenolepis</i>	1
Carcharinid, ? <i>Prionace glauca</i>	2
Squids	1

The above eight killer whales with remnants of marine mammals in their stomachs included six adult males, one adult female.(California),

and one immature male (Gulf of Alaska). The stomach of five adult males contained only the remnants of marine mammals while the sixth additionally had remnants of squids. The stomachs of the adult female and the immature male had only the remnants of fish, including sharks. It may be assumed that male killer whales feed predominantly on marine mammals.

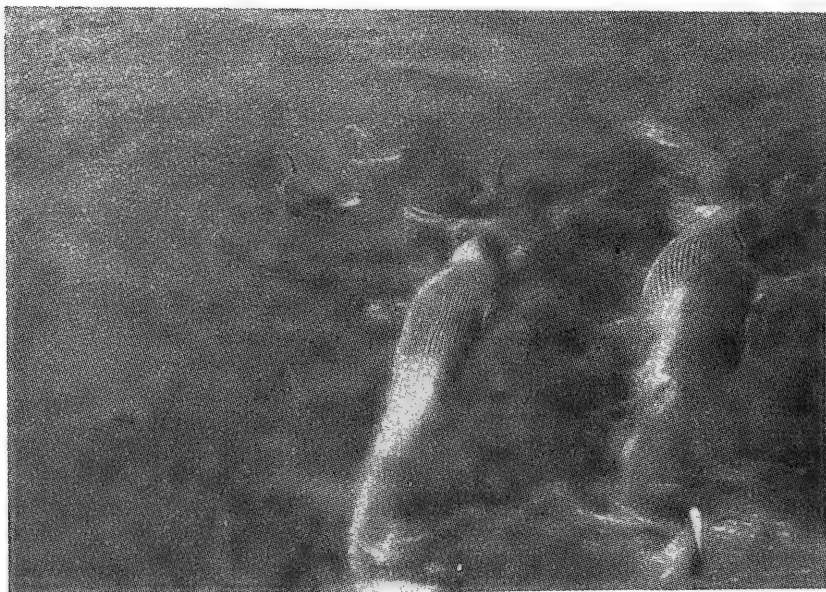
The mammals were represented mostly by the remnants of one, less frequently two, and only in one case (elephant seal) four animals in the same stomach. All of them were thoroughly digested, since mostly the teeth, nails, and sometimes ribs or skin remnants were found. Minke whale was represented by baleen plates and chunks of blubber. Layer formations on the teeth helped to establish the age of some of the pinnipeds consumed by killer whales. Thus the stomach of a male killer whale 7.6 m long contained the remnants of a nine-year-old sea lion, of another male killer whale 6.86 m long the remnants of a one-year-old Steller's sea lion (probable weight of the animal 90 kg), and of yet another male 7.24 m long a two-year-old (probably) Steller's sea lion (Rice, 1968).

The hunting of sea lions by killer whales has been described as follows: a group of five killer whales chased a large male sea lion on May 25, 1965 in the San Francisco region. The adult killer whale in the group (it also contained calves) continuously lay under the sea lion, or above it when the sea lion dived. From time to time, the killer whales struck the quarry with their bodies or attempted to crush it. The sea lion jumped from side to side, sometimes leaped out of the water, and eventually became exhausted. At this point one killer whale swam to its right, another underneath it, while a third grabbed the quarry with its teeth and towed it under water. That was the last sighting of the sea lion on the water surface. This happened very close to a ship following the attacking killer whales; the latter paid no attention to the ship behind them. In another case, one of the six killer whales (the group contained two calves and one adult male) appeared on the water surface holding a small sea lion in its mouth. The nature of mammal remnants seen in the stomach of killer whales suggests that they dismember large animals before ingestion but swallow smaller prey entire (Rice, 1968).

Reports of killer whales attacking large whales require documentary proof. In the Antarctic, near a whaling base, groups of killer whales were noticed floating alongside fin whales, humpback whales, and other species of baleen whales time and again. Yet no attempts by the killer whales to attack the others were ever recorded. Concomitantly, the other whales (even when alone) never exhibited signs of restlessness on the approach of a herd of killer whales. However, killer whales regularly tore out the tongues of dead and air-filled whales with mouths wide open

(Fig. 294). The carnivores were bold enough to tear out the tongues of killed whales tied to the board of a whale boat towing them to the base. Often the killer whales almost wholly consumed the tongues of whale carcasses stocked as feed for the whale base. Attempts to drive away the killer whales by throwing various objects at them from the whale boat or even by opening fire were almost of no avail. The tongue of whales weighs two to three tons and contains a large amount of fat; thus killer whales quite often cause serious losses to whale hunters by snatching away the valuable tongues. Yet there are no reports of killer whales attempting to tear off chunks of blubber from a whale carcass or to snatch its fins (V.A. Arsen'ev). Apparently, there is no justification for ascribing the various damages caused to dead whales to the activity of killer whales.

The killer whale is generally described as an unusually greedy carnivore and fantastic figures are cited about the quantum of food found in its stomach. The stomach of a 6.5-m long killer whale purportedly contained "five or six seals and semidigested remains of another six or seven seals and thirteen harbor porpoises; in addition, there were two nearly whole seals in the gullet" (Tomilin, 1957). If the average weight of these animals is taken as even 30 kg, the stomach contents of this killer whale should have weighed at least 600 kg, while the contents of



514 Fig. 294. Killer whales tearing out the tongues of dead whales (photograph by V.A. Zemskii).

a closely packed stomach of a 20-m long fin whale would weigh about 1,000 kilograms. The killer whale is no doubt a powerful and dangerous carnivore but its food habits have yet to be properly studied.

Behavior. Killer whales usually live in groups of a few to 100 or more animals. They are encountered in the open sea as well as close to coasts. Of the 567 killer whales caught in the waters of Japan, 391 (69%) were killed within the 30-mile zone, 101 (17.8%) at a distance of 31 to 60 miles, and 36 (6.3%) beyond 60 miles from the coasts. The distance at which the remaining 39 killer whales were killed could not be ascertained. However, the spread of the party hunting for killer whales (along with other species of cetaceans) is also of some importance in such cases (Nishiwaki and Handa, 1958).

Some instances are known of the transgression of killer whales into a river at a distance of a few tens of kilometers from the estuary in which the animals were confined to a freshwater zone, sometimes for a few weeks.

While feeding, killer whales move at 5-7 miles per hour and during migrations at 15-17 miles per hour. It has been noticed quite often that
 515 large groups of killer whales move in a broad front or even in columns (Fig. 295). They usually spend 2 to 5-6 min under the water and perform five to six brief spells of exhalation/inhalation in the interval between



515 Fig. 295. Killer whales at sea. Pacific Ocean, 1948 (photograph by M.M. Sleptsov).

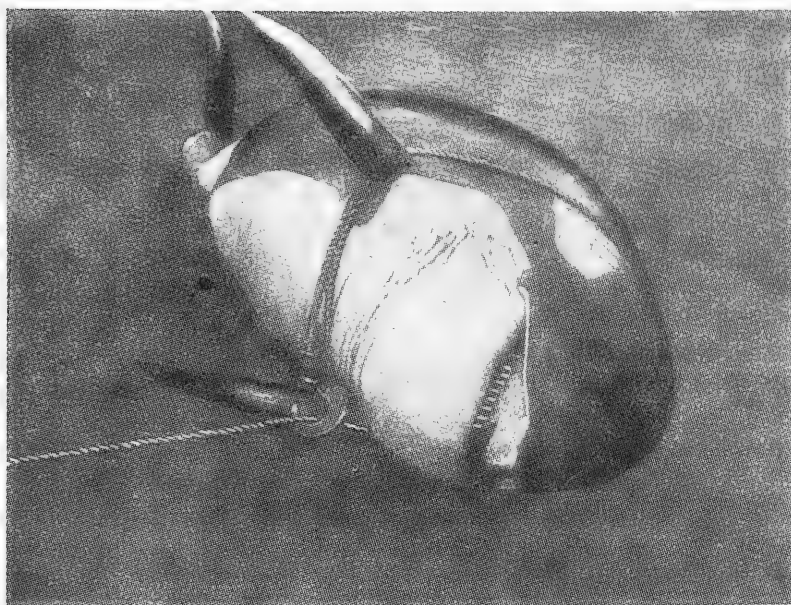
dives. Sometimes they remain on the water surface for quite a long time, with their high dorsal fins visible above the sea level throughout this period. The blow produced by the killer whale is rather low, not more than 2 m high.

The strong affinity of adult animals for each other and their calves is a characteristic feature. It is difficult to break up a herd of killer whales and quite often many animals of a given group can only be caught on just one side of the ship. The animals are more active in warm water (20–25°C) and become sluggish as the water temperature drops to 10–15°C. It is easy to catch the killer whale at this time and hence most of those caught in the waters of Japan come from the northern part of the country. This fact notwithstanding, killer whales do transgress into polar waters and do not shirk from ice, although none have been sighted among compact ice.

Migrations. The courses and periods of seasonal migrations of killer whales have not been studied. They are sighted over much of the range throughout the year but in the polar sections of the Northern and Southern hemispheres apparently only in the summer months. The killer whales seen on the coasts of the Chukchi Peninsula in June abandon these waters by November–December (Nikulin, 1946). They inhabit Hudson Bay, Fox Basin, and Davis Strait too only in the summer period. Killer whales, like other species of cetaceans, are encountered in the waters of Antarctica only in the summer months and abandon them altogether in winter. Killer whales may continue to remain in the winter months even at high latitudes only at such places in the oceans which fall under the influence of powerful warm-water currents (for example, the Gulf Stream).

In the waters of Japan, the bulk of the killer whales are caught from April through November inclusive while the catch is insignificant from December through April. More killer whales are caught on the coasts of Hokkaido (northern coast, Sea of Okhotsk; southeastern coast, Pacific Ocean), fewer on the northeastern coast of Honshu (38–40° N lat.), and even fewer on the southeastern coast of this island (33–35° N lat.). In the Sea of Japan, there is virtually no hunting of the killer whale (Nishiwaki and Handa, 1958).

Reproduction. Mating of killer whales was observed in June and July and births in spring and summer (Scheffer and Slipp, 1948) although the view is prevalent that parturition occurs mainly in autumn. Embryos 27 to 222 cm long were found in July–August among killer whales of the Kuril Islands. At this time, simultaneous with gestating females, four lactating mothers were found. They had probably calved in July (Ivanova, 1961c). A nearly mature embryo measured 208 cm in length while the



516 Fig. 296. Killer whale on the deck of a whaling base (photograph by V.A. Zemskii).

largest was 274 cm long. The smallest of the measured calves were 236, 246, 251, and 274 cm. Such measurements are evidently characteristic of newborn calves. It has been suggested that gestation among the killer whales can extend for 16 months but the maximum number of births has been recorded in May to July (an instance of mating was photographed from an airplane on June 22, 1957) although mating and parturition can occur in the other summer months as well. Additional documented information is required to resolve the questions of the duration of gestation and periods of mating and parturition.

The duration of lactation has not been established.

By the time it is one year of age, the killer whale calf has reached a length of about 350 cm. The average length of 320 males caught in the waters of Japan was 6.4 m, with the largest 9.45 m long. The average length of 247 females was 6.1 m, with the maximum length at 8.23 m. Most of the males caught varied in length from 5.5-7.6 m and females 5.5-6.7 m. Of the 567 killer whales caught from 1948 through 1957, 320 were males (56.4%) and 247 females (43.6%). The sex ratio is evidently close to 1:1 (Nishiwaki and Handa, 1958).

Enemies, diseases, parasites, mortality, and competitors. The killer whale has no enemies. The diseases known in them are bone tumors

(detected in skeletons preserved in museums) and dental caries. Ectoparasites are not known. Eight species of endoparasites have been reported: two species of trematodes, one species of cestode, three species of nematodes, and two species of acanthocephalans.

The trematode *Fasciola skrjabini* Delamure was found in the bile ducts of the liver of the killer whale and the Minke whale in the North Atlantic. The intestine of a killer whale in the fore-Kuril waters revealed the presence of the trematode *Leucasiella subtilia* A. Skrjabin. The cestode *Trigonocotyle spasskyi* Gubanov was found in the small intestine of whales only from the Sea of Okhotsk (Kuril waters). The widely prevalent nematode *Anisakis* (*Anisakis*) *simplex* Rudolphi, parasitizing the gullet, stomach, and intestine, was detected in 10 other species of toothed whales, two species of baleen whales, and in Steller's sea lion in addition to the killer whale. The nematode *Anisakis pacificus* A. Skrjabin was
 517 found in the stomach of killer whales (and also sperm whales and fin whales) in the waters of the Kuril Islands. Another species of nematode, *Anisakis* sp., found in the killer whale, has eluded precise identification. The acanthocephalan *Bolbosoma physeteris* Gubanov, parasitizing the intestine was found in killer whales from the Sea of Okhotsk and *Bolbosoma nipponicum* Yamaguti from the Kula Gulf (?) (Margolis, 1954; Delamure, 1955; A. Skrjabin, 1958, 1959, 1960).

Field characteristics. A very high dorsal fin, rising to a height of over 1 m in males, distinguishes the killer whale from all other cetaceans. At a close distance, bright white oval patches can be seen on the temples and a large white patch posterior to the dorsal fin. Killer whales are usually confined to groups. Quite often, the groups present a broad front or move in a column. (V.A.)

Economic Importance

In spite of the comparative abundance of killer whales in the World Ocean, their hunting has acquired no economic importance. Killer whales are mostly caught casually during hunts for other cetaceans, such as beaked whales, Minke whales, and various other species of dolphins. A fairly organized hunting of killer whales exists only in Norway and Japan with whaleboats specially designed for small whales (Minke whale, bottlenose whale and other beaked whales, pilot whale, and killer whale). Data on killer whale hunting for several years are given in Table 40.

As mentioned, Norwegian and Japanese hunting is carried out in specially designed craft equipped with small-bore harpoon guns. In the Soviet Union, the killer whale is hunted from the large whaleboats used in hunts for large whales in the Far Eastern waters as well as in the

Table 40. Magnitude of killer whale hunting (international whaling statistics)

Year	Norway	Japan	USSR	Year	Norway	Japan	USSR
1948	27	27	3	1959	69	36	36
1949	34	43	28	1960	82	48	45
1950	12	18	24	1961	111	54	4
1951	24	67	23	1962	124	47	7
1952	13	54	19	1963	90	43	4
1953	9	65	25	1964	77	99	
1954	13	109	4	1965	104	169	
1955	26	85	15	1966	161	137	9
1956	40	38	67	1967	36	101	4
1957	48	78	30	1968	86	22	
1958	39	73	25				

Antarctic. In other countries, some stray killer whales are caught incidentally.

The fat of the killer whale, like that of other toothed whales, is used for commercial purposes. The skin of the killer whale is regarded as superior to that of other toothed whales and can be used for producing leather goods. The rest of the carcass is used in the preparation of feed or in fertilizer meal. (V.A.)

518

Genus of Risso's Dolphins

Genus *Grampus* Gray, 1828

1828. *Grampus*. Gray. Spicilegia. Zoologica, I, p. 2. *Delphinus griseus* G. Cuvier, 1812.

1933. *Grampidelphis*. Iredale and Troughton. Rec. Austral. Mus., 19, p. 31. Substituted for *Grampus* Gray, 1846.¹¹ (V.H.)

Dolphins of medium proportions, with a body length up to 430 cm.

The head is rounded anteriorly and no "beak" is perceptible. The high dorsal fin, located almost midbody, is notched along the posterior margin. The flippers are long and narrow.

The body color is basically gray.

The rostrum is broad; its length is shorter than the cranial section of the skull. The proximal portions of the broad premaxillae form a prominence. The pterygoid bones are adjacent. The nasal and frontal bones form a crest posterior to the nares. The mandibular symphysis is short. In most of these animals, teeth are present only in the anterior portion of the lower jaw in two to seven pairs (0-2 in the upper jaw).

¹¹ See footnote on p. 680.

Vertebrae 68-69. Phalangeal formulae: I₂, II₈₋₁₀, III₅₋₈, IV₃₋₅, and V₁.

Very little is known about the biology of these animals. They feed on cephalopods and live singly or in small groups.

They inhabit the warm and moderate waters of both hemispheres but are few in numbers everywhere. They are not caught in the waters of the USSR but might possibly occur in the waters of the Far East.

The genus comprises a single species: Risso's dolphin, *Grampus griseus* G. Cuvier, 1812. (V.S.)

RISSO'S DOLPHIN

Grampus griseus G. Cuvier, 1812

1812. *Delphinus griseus*. G. Cuvier. Ann. Mus. Hist. Nat., Paris, 19, p. 13. Brest, France.
1822. *Delphinus rissoanus*. Desmarest. Mammalogie, p. 519. Mediterranean Sea, Nice.
1866. *Globicephalus chinensis*. Gray. Cat. Seals and Whales Brit. Mus., p. 323. China Sea.
1873. *Grampus stearnsii*. Dall. Proc. Calif. Ac. Sc., 5, p. 13. Monterey, California. (V.H.)

Diagnosis

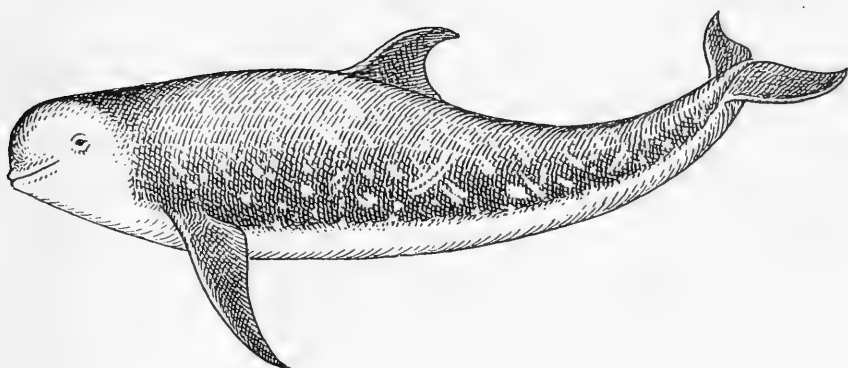
Only species of the genus.

Description

Body compact. The highly developed adipose body [melon] imparts a circular shape to the head while the frontal portion slightly projects anteriorly. The lower jaw is shorter than the upper. The oral cavity runs obliquely upward from front to back. The flippers are long, constituting 13.9 to 19.6% of the body length, narrow, crescent-shaped, and pointed at the ends (Fig. 297).

The body color varies from gray to blackish-gray, gradually turning lighter from the dorsum toward the belly. The head is also lighter in color than the dorsum but all the fins are the same color as the dorsum. Small light-colored spots and bands on the skin are the result of various damages. Hairs (up to eight) are sometimes preserved on the head of young animals.

- 519 The diameter of the teeth of adult dolphins can reach 1.5 cm and the height almost 4 cm (root and crown). The loss of teeth in the upper



519 Fig. 297. Risso's dolphin, *Grampus griseus* (figure by N.N. Kondakov).

jaw is a recent phylogenetic phenomenon and apparently the result of these animals feeding on cephalopods (Tomilin, 1957).

Cervical vertebrae 7, thoracic 12-13, lumbar 18-19, and caudal 30-31. The sections of the vertebral column constitute the following percentage ratio to its total length: cervical 2.5, thoracic 24.5, lumbar 29, and caudal 44 (Slijper, 1936).

The basic body measurements of three adult female Risso's dolphins (Tomilin, 1957; Pilleri, 1969) are respectively (in cm): body length 330, 320, and 275; distance from tip of snout to blowhole 43 and 48, up to dorsal fin 127, 119, and 95, up to base of flippers 56 and 64; length of flippers 54, 61, and 45; maximum width of flippers 22 and 17; height of dorsal fin 34, 41, and 40; length of base of dorsal fin 56 and 35; and width of caudal flukes 74 and 79.

The average skull measurements based on nine skulls (Fig. 298) of adults (Tomilin, 1957) are (in cm): condylobasal length 50, length of rostrum 25, width of rostrum at base 20, and length of lower jaw 39. (V.S.)

Geographic Distribution

Warm and temperate waters of the Northern and Southern hemispheres.

Geographic Range in the USSR (Fig. 299)

Coastal waters of the Kuril range, mainly its southern part (Iturup and Shpanberg Islands)¹², and the Commander Islands.

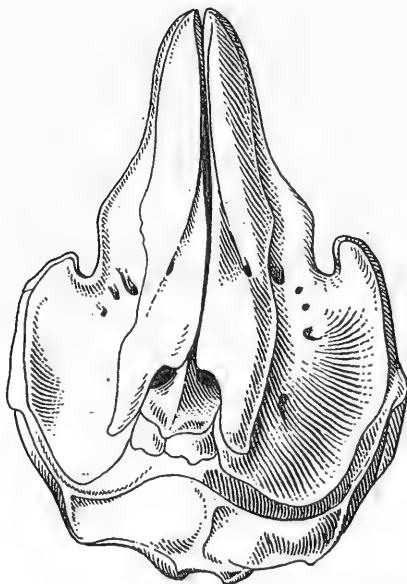
¹² Finds reported for the Kuril Islands (Sleptsov, 1952) have yet to be confirmed with specimens.

520 *Geographic Range outside the USSR (Fig. 300)*

Gulf of Maine and the coastal waters of New Jersey state along the American coast of the North Atlantic (the range may be more extensive but precise data are not available). In the eastern part of the Atlantic Ocean, the range extends from the North Sea (waters of Great Britain, Schleswig in the Federal Republic of Germany, Denmark, and western coast of southern Sweden in Bohus Bay) and Ireland down to South Africa. Mediterranean Sea in the east including the Adriatic. In the eastern part of the Pacific Ocean, from British Columbia to Baja California (Mexico) and waters of the Chilean coast; in the western part of this ocean from the Commander Islands (?) and Kuril Islands and Japan to the seas of China. Waters of New Zealand and Australia (New South Wales), the Indian Ocean, and the Red Sea. (V.A.)

Geographic Variation

Not known.



Biology

In all probability, this species is not very numerous throughout its range. Some species of cephalopods constitute its main food. Remnants of other food items have not been detected in the stomach of Risso's dolphins. In search of cephalopods, this dolphin makes comparatively long dives and remains on the water surface longer than other species. It mainly inhabits the open seas. In most cases, it swims singly, in pairs or in small groups. These dolphins gather in herds of a few tens of animals only occasionally at places of food concentration.

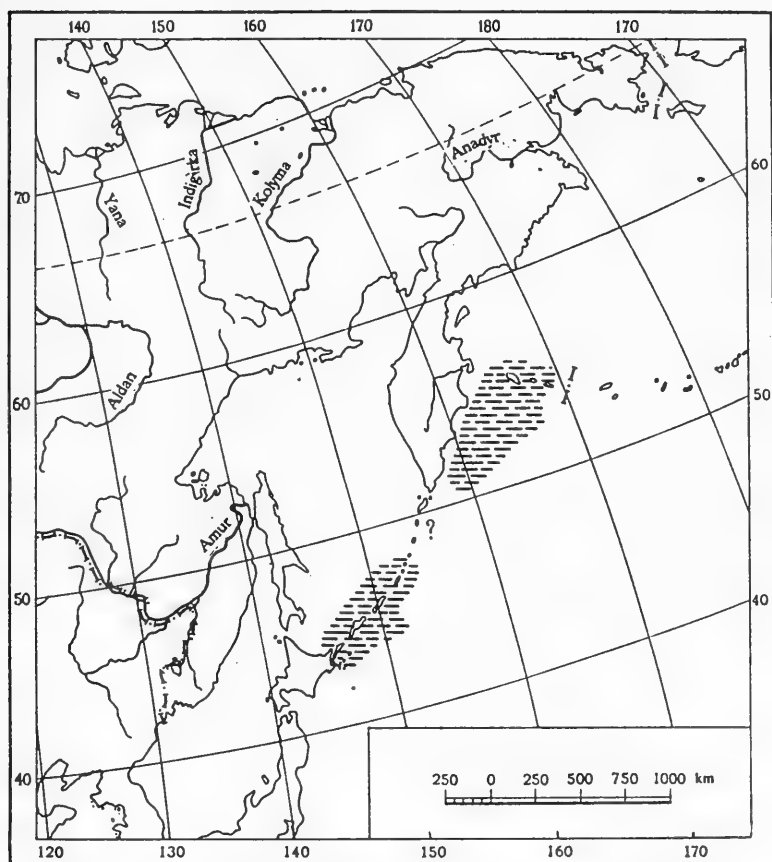


Fig. 299. Range of Risso's dolphin, *Grampus griseus*, in the USSR (V.A. Arsen'ev).

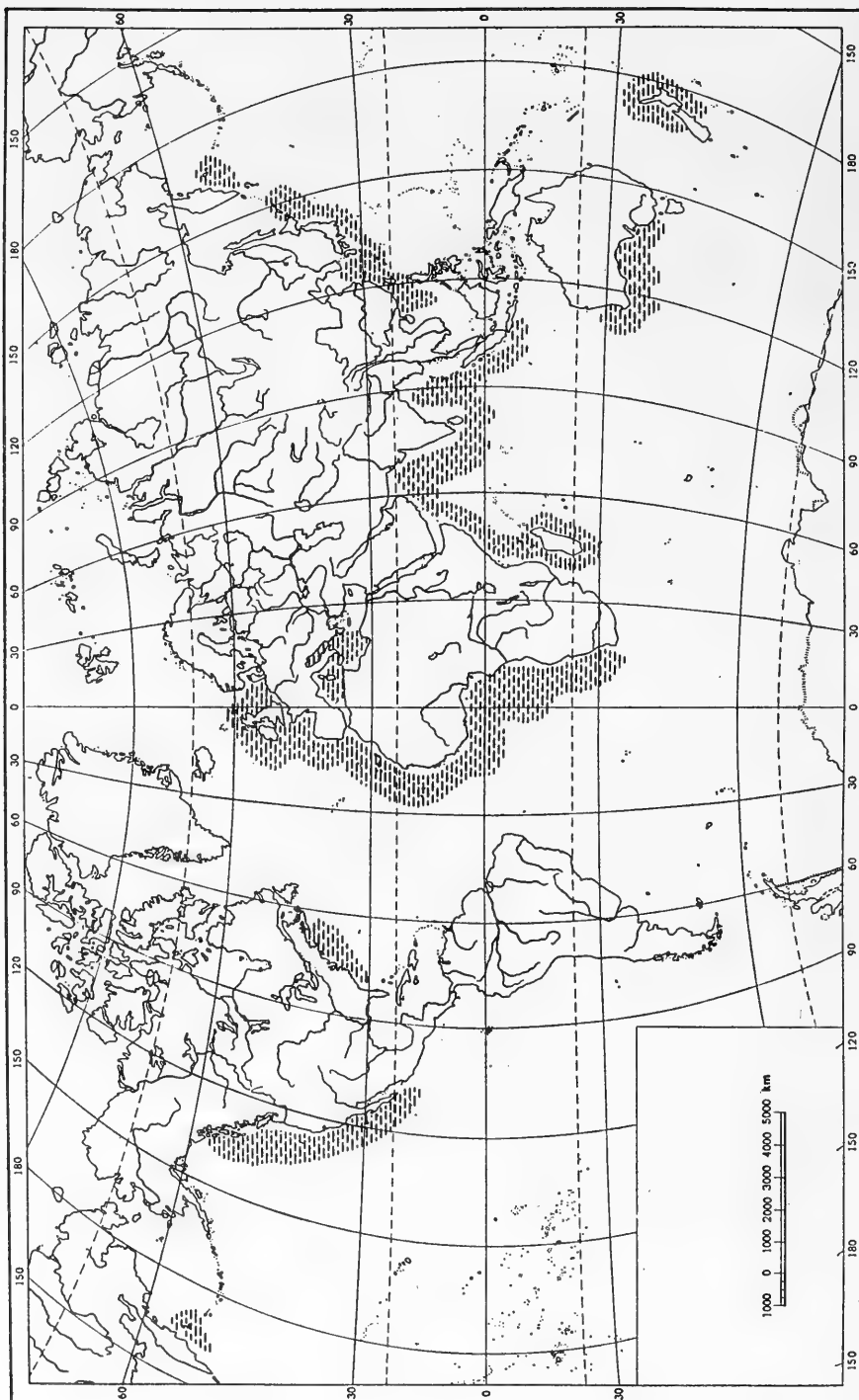


Fig. 300. Species range of Risso's dolphin, *Grampus griseus* (V.A. Arsen'ev).

Migrations have not been established. It is known that these dolphins live year-round in the Mediterranean Sea and in European waters, although some variations in their numerical strength have been recorded in different months.

According to some fragmentary information, parturition occurs in the winter months in comparatively warm waters. The newborn calf average 150 cm in length.

Three species of endoparasites are known. The cestode *Phyllobothrium delphini* Bosc localizes in the skin of Risso's dolphin and also six other species of toothed cetaceans, the bowhead whale, and Weddell's seal. It has been detected in these animals at many points in the Atlantic Ocean, the Mediterranean Sea, waters of the Commander Islands and Australia, the Pacific Ocean, and the Antarctic. The nematode *Crassicauda grampicola* Johnston and Mawson was detected only among Risso's dolphins in the waters of Australia. *Stenurus minor* Kühn parasitizes the bronchi, tympanic cavity, and blood vessels (Delamure, 1955).

Risso's dolphin is of no economic importance. (V.A.)

Genus of Pilot Whales

Genus *Globicephala* Lesson, 1828

1828. *Globicephala*. Lesson. Nat. Hist. Mamm. Diseaux Depuis 1788, Cétacées, p. 441. *Delphinus deductor* Scoresby = *Delphinus melas* Traill.

1828. *Globicephalus*. Lesson. Férussac Bull. Sci. Nat., 16, p. 116. Substituted for *Globicephala* Lesson, 1828.

1884. *Globiceps*. Flower. Proc. Zool. Soc. London, 1883, p. 508. Substituted for *Globicephala* Lesson, 1828. Nom. praeocc. (V.H.)

Large dolphins, with a body length of up to 6.5 m.

The head is rounded and a beak faintly perceptible. The dorsal fin is low with a curved posterior margin. The flippers are narrow and long.

The body is dark, grayish-blue, or black.

The skull is broad and slightly flattened dorsoventrally. The rostrum is almost as long as the cranium. The premaxillae are very broad. The pterygoid bones are adjacent. The nasal bones project into the frontal and lie above the level of all the other bones. Teeth $\frac{7-13}{7-13}$, present in the anterior half of the jaws. With advancing age, the teeth may wear out and fall out. Vertebrae 58-59. The sternum comprises three to four sections. Five of the 11 pairs of ribs articulate with the sternum. Phalangeal formula: I_{3-4} , II_{9-14} , III_{9-11} , IV_{1-2} .

These whales feed on large invertebrates (mainly cephalopods) and schooling fish (teutho-ichthyophagous). Periods of mating and

parturition are protracted. Gestation and lactation continue for about a year each. Members of this genus are confined to large herds of a hundred or more animals.

The range of these whales covers all the seas except the polar. In the USSR, they might possibly occur in the Barents Sea and in the waters of the Far East.

Fossil remains have been detected in the Pleistocene of North America.

The genus comprises a single species: the (common) pilot whale, *G. melaena* Traill, 1809.

Sometimes pilot whales are classified into two species, *G. melaena* and *G. macrorhyncha* Gray, 1846 (Rice and Scheffer, 1968*), or into three species, i.e., *G. scammoni* Cope, 1869, in addition to the two aforesaid. (V.S.)

PILOT WHALE

523

Globicephala melaena Traill, 1809

- 1809. *Delphinus melas*. Traill. Nicholson's Journ. Philos., 22, p. 81. Pomona Island, Orkney Islands.
- 1812. *Delphinus globiceps*. G. Cuvier. Ann. Mus. Hist. Nat., Paris, 19, p. 14. France.
- 1820. *Delphinus deductor*. Scoresby. Account Arctic regions, I, p. 496. North Atlantic.
- 1824. *Delphinus grinda*. Lungbye. Kongl. Danske Vedensk. Selsk. Afh. I, p. XI. North Atlantic.
- 1846. *Globicephala sieboldii*. Gray. Zoology Voyage Erebus and Terror, I, p. 142. Near Nagasaki, Japan.
- 1869. *Globicephalus scammoni*. Cope. Proc. Ac. Sc. Philadelphia, 21, p. 21. California (10°N lat.).
- 1871. *Globicephalus sibo*. Gray. Suppl. Cat. Seals and Whales Brit. Mus., p. 85. Japan.
- 1898. *Globicephala melaene*. Thomas. Zoologist, (4), 2, p. 99. Masculine form *melas* for the feminine of the genus, conforming to the generic name. (V.H.)

Diagnosis

Only species of the genus.

Description

The body is elongated and slightly thickset in the anterior half. The head is rounded with a projecting frontal part as a result of the highly

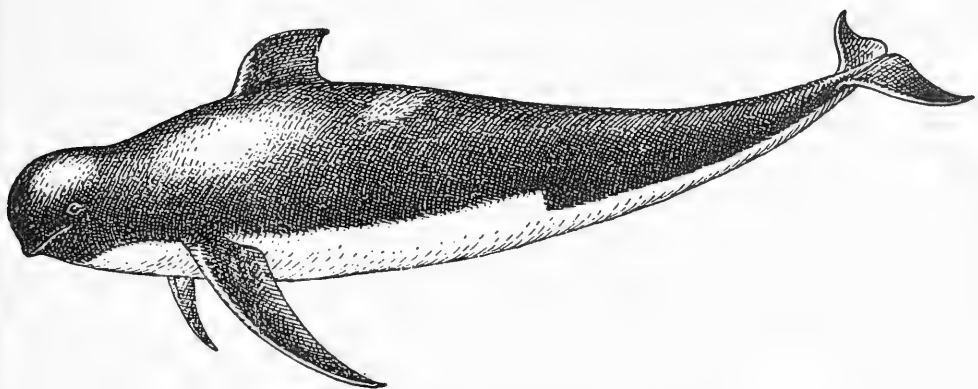
developed adipose body [melon]. The oral cavity runs from front to back with an inclination of roughly $30-45^\circ$ to the longitudinal axis of the body from the bottom upward. The upper jaw is longer than the lower one. The blowhole is slightly displaced left of the midline. The long and low dorsal fin is located almost at the boundary of the anterior third of the trunk. The length of the fin at the base is not less than 1.5-2 times its height. Long flippers reach one-fourth of the body length (Fig. 301).

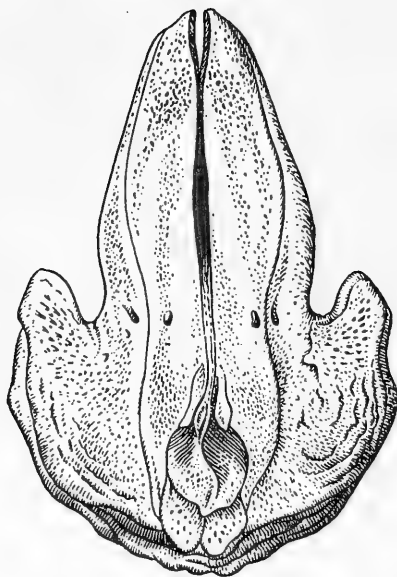
The upper portion of the body is darker in color than the underside. A narrow gray band enlarges into a patch between the flippers midabdomen and on the throat. A newborn pilot whale is gray but soon turns black. With age, high longitudinal ventral and dorsal keels form on the caudal stem of males. The adipose body [melon] of the head and the hump between the head and dorsal fin are larger in males than in females. Embryos sport three to six hairs on each side of the snout.

Cervical vertebrae 7, thoracic 11, lumbar 12-14, and caudal 28-29. The first five or six cervical vertebrae are fused.

The main body measurements of an adult male pilot whale caught off the coast of Virginia (North Atlantic) (Tomilin, 1957) are (in cm): body length 465; distance from tip of snout to blowhole 54, up to anal opening 318, and up to base of flippers 91; length of flippers 76, maximum width of flippers 25; length of base of dorsal fin 79; height of dorsal fin 35; and width of caudal flukes 117. The largest male measured 6.5 m in length and the female 6.1 m.

The main measurements of six skulls (Fig. 302) of adult pilot whales averaged (Tomilin, 1957) (in cm): condylobasal length 63 (six measurements), zygomatic width 41 (one), length of rostrum 32 (six), width of rostrum at base 23 (six), and length of lower jaw 49 (two).





524 Fig. 302. Skull of pilot whale, *Globicephala melaena* (figure by N.N. Kondakov).

The relative dimensions of the rostrum, the width of the skull at the level of the orbits, and the width of the rostrum at its base and center increase with age (Tomilin, 1957). (V.S.)

Geographic Distribution

Almost all the seas and oceans from the Arctic to the Antarctic except the frozen seas of high latitudes.

Geographic Range in the USSR (Fig. 303)

Southwestern part of the Barents Sea, especially the waters of Rybachii peninsula (irregular transgressions; Nemirovich-Danchenko, 1877; Chapskii, 1941), waters of the Kuril range, and possibly southeastern Kamchatka, Commander Islands, and the Sea of Japan (La Perouse Strait).

Geographic Range outside the USSR

In the North Atlantic it is found along the American coast from Delaware Bay to Newfoundland, Labrador, Davis Strait (up to 70°N lat.) and the southeastern coast of Greenland (67°N lat.). In the eastern part it occurs

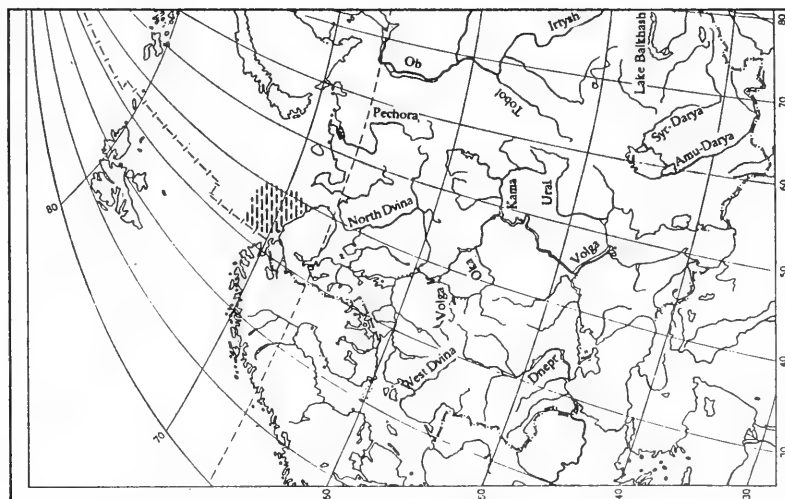
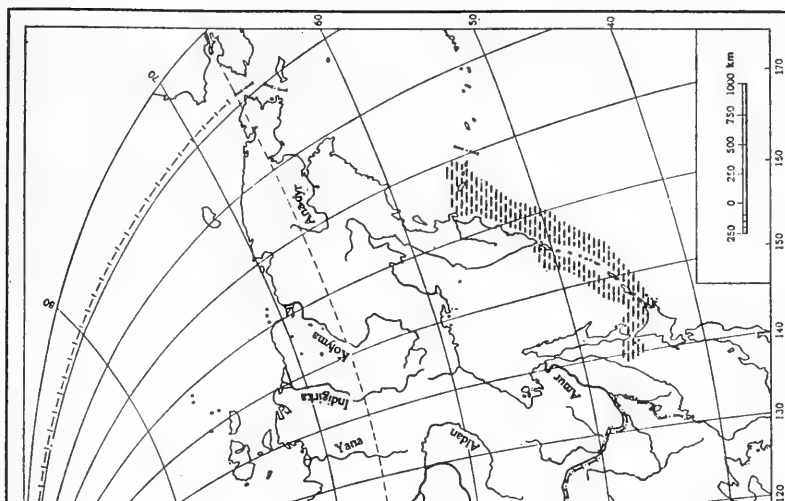


Fig. 303. Range of pilot whale, *Globicephala melaleuca*, in the USSR (V.A. Arsen'ev).

from Iceland and northwestern Norway along the entire coast south up to Madeira,¹³ Mediterranean Sea. In the south, evidently inhabits waters up to 60°S lat. in the Atlantic (Fig. 304).

525 In the North Pacific Ocean, up to the waters of southeastern China to the west and south; in the eastern part of the ocean from the Aleutian Islands and Alaskan peninsula down to Mexico (Baja California). In the tropical zone, the pilot whale is probably distributed over large expanses far away from the coasts.

In the Southern hemisphere, it is known on the coasts of India (Bay of Bengal), Java, Guatemala, Ecuador, Peru, Chile, Australia, Tasmania, New Zealand, Kerguelen Island, and South Africa. The range apparently reaches 50 to 60°S lat. (Sergeant and Fisher, 1957; Tomilin, 1957; Brown, 1961; Hershkovitz, 1966; Nishiwaki, 1967). (V.A.)

Geographic Variation

Some authors recognize up to five or six subspecies but their validity (even of the two subspecies mentioned below, the most sharply manifested) is usually questioned or contradicted (Hershkovitz, 1966). Distant migrations characteristic of the species result in a thorough mix-up over the entire extremely extensive but essentially single range. Deviations in the picture of distribution of the various forms, especially of those given below, are highly significant (see Tomilin, 1957, 1962; Hershkovitz, 1966).

Two subspecies can be recognized in the waters of the Soviet Union:
1. **Common, or Atlantic pilot whale**, *G. m. melaena* Traill, 1809 (syns. *melas*, *globiceps*, *deductor*).

Thirteen pairs of teeth in each jaw; the white band on the ventral side of the body is broadened in the region of the flippers, and a large white, anchor-shaped patch occurs on the throat.

Southeastern part of the Barents Sea, especially waters of the Rybachii peninsula.

¹³ References to habitation in the Baltic Sea are very general and neither positive nor reliable. They are mainly communications from one author to another and it is very difficult to identify the actual sources. More positive references are available only for the waters of Denmark (Jutland peninsula) and southwestern Sweden, i.e., the same section of the coast facing Jutland. Such references usually extend to the entire Baltic Sea. For the waters of the German Democratic Republic and Poland, there are no direct references to the habitation of the pilot whale and this species is not included among the cetaceans inhabiting these waters (Gentshel', 1937; van den Brink, 1958; Koval'skii, 1964; Siivonen, 1968). Transgressions into the basin of the Baltic Sea proper might occur very rarely but the appearance of this animal in our waters far into the northeast is highly improbable. (V.H.)

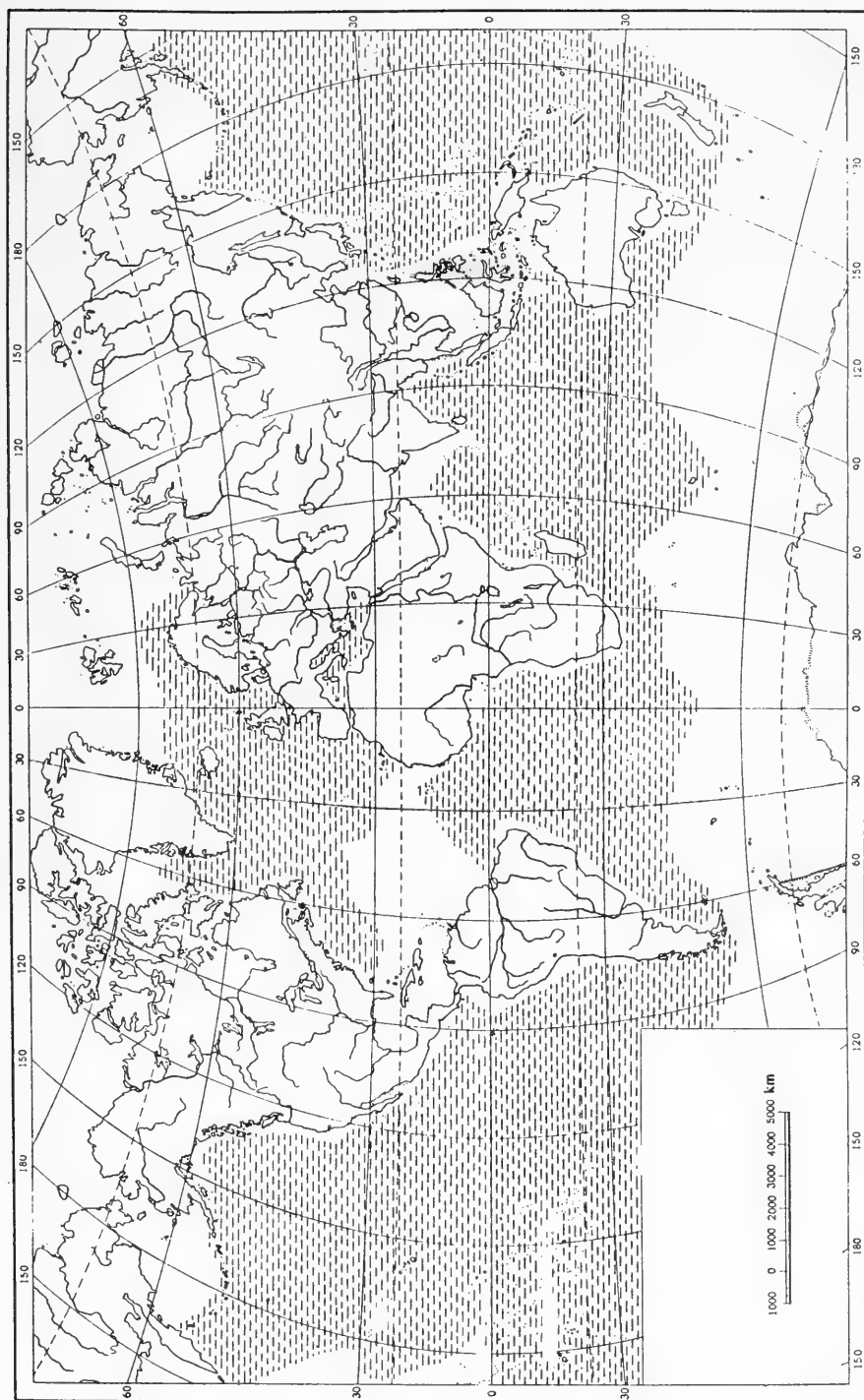


Fig. 304. Species range of the pilot whale, *Globicephala melaena* (V.A. Arsen'ev).

Outside the USSR, it is encountered in the North Atlantic Ocean up to southern Greenland (almost 70°N lat.).¹⁴

2. **Black, or Pacific pilot whale**, *G. m. sieboldii* Gray, 1846 (syns. *scammoni*, *sibo*). Seven or eight pairs of teeth in each jaw. Color black, with no white markings.

Waters of Kuril Islands (not known more accurately), probably Kamchatka, Commander Islands, and the Sea of Japan (La Perouse Strait).

Outside the USSR, this subspecies is encountered in the North Pacific Ocean up to the Yangtze estuary in the west and from the Aleutian Islands and Alaska to Guatemala in the east.

Pilot whales belonging to two or three other subspecies of this species are sometimes listed as inhabitants of the Southern hemisphere (Tomilin, 1962; Nishiwaki, 1966). (V.A.)

Biology

Population. The pilot whale can be reckoned as a relatively abundant species. In some regions of the range (North Atlantic, waters of Japan, and South Pacific Ocean), this dolphin often forms herds a thousand or more strong. It is difficult to indicate the regions of maximum population of the pilot whale.

528 *Food.* Squids serve as the main food. In the waters of Newfoundland, the pilot whale consumes the squid *Illex illicebrosus* almost exclusively. This squid is remarkably abundant here. In the summer months, pilot whales approach the island coasts chasing after it. In the absence of squids, pilot whales consume cod (in small quantities). In a Florida oceanarium, a young pilot whale initially refused to eat fish but after sometime was taught to accept it. In the waters in which *I. illicebrosus* is not available, the stomach of pilot whales contained the remnants of other species of squids, e.g., *Ommatostrephes (Todarodes) sagittatus*, and some species of the family Onychoteuthidae. Otoliths of mackerels (*Caranx trachurus*), small flounders (Pleuronectidae), and herrings have been found from time to time.

Young pilot whales feed on much smaller squids than the adults do. The nearly identical degree of digestion of the food in the stomach of pilot whales caught at the same time suggests that the entire herd feeds together. By converting the quantum of the remnants of squids and fishes into the average weight of intake, it was established that the stomach of a pilot whale of medium proportions (length 396 cm) held 12-14 kg

¹⁴ The following distribution has been given for this form: "Atlantic, Pacific, and Indian oceans from 70°N lat. to roughly 60°S lat." (Hershkovitz, 1966).

of food. The stomach of a female 247 cm long contained 155 squids weighing in toto 27 kg. In an oceanarium, a male pilot whale 525 cm in length daily consumed an average of 45 kg of squids and mackerel, while a female 396 cm long consumed up to 36 kg; another female (366 cm long) ate 18 kg three times a day. Apparently, under natural conditions, the pilot whale may fill its stomach two or three times a day. Such voracious feeding is only resorted to, however, during the three or four summer months when immense concentrations of squids are available. During the rest of the year the daily ration of the pilot whale is quite modest.

At a daily consumption of 27 kg, the annual food requirements are about 10 tons. Taking the weight of a pilot whale of medium proportions (396 cm long) as 830 kg, its annual food intake represents 11.5 times the weight of the animal itself. The daily quantum of food consumed by the dolphin constitutes 3 to 5% of the animal's body weight.

Observations on three pilot whales in a basin showed that they fed only at night and rested during the day. Under natural conditions in Newfoundland, pilot whales were observed feeding during the day also. The stomach of a pilot whale caught between 7:00 and 11:00 a.m. revealed food recently consumed. It is probable that the long summer day in these latitudes causes the squids to rise to the upper horizon not only at night, but also during the day, which enables successful catches by the pilot whales (Sergeant and Fisher, 1957; Tomilin, 1957).

Behavior. Pilot whales usually live in herds of some 20 animals, on average, but sometimes do form herds of up to a thousand or even several thousands of animals. They dive for comparatively longer periods and surface sometimes 8-10 times in a row, producing low (up to 1.5 m high) bushy blows. They never display the caudal flukes and never leap free of the water surface. Large herds of pilot whales are formed from individual groups of 15-25 animals each.

The composition of the herds varies. Thus a herd of 16 pilot whales comprised 7 males and 8 females (the sex of one whale could not be ascertained). Of the seven males, three were mature, three immature, and one a newborn calf. The eight females comprised six mature, one on the threshold of maturity, and one newborn. This was a mixed herd. The predominance of mature females over mature males suggests polygamy. The ratio between the adult males (472 cm and above) and adult females (336 cm and above) was close to 1:3.

Another herd studied consisted of 14 pilot whales which comprised 10 males and 4 females. The length of nine males was typical of mature animals and all the four females were large, presumably "old". Such a herd could be called a "bachelor" group, made up in all probability of

animals which did not take part in reproduction in that particular year (Sergeant, 1962b).

Pilot whales often form mixed herds together with some species of very small dolphins. In such herds, apart from the distinct presence of the shorthead dolphin [*Lagenorhynchus electra*] and the bottlenose dolphin, other species of dolphin may also be present. When such a herd
529 approaches a ship standing in the sea, all the small dolphins disappear into the water after some time while the pilot whales invariably continue to remain close to the ship (Brown, 1961).

Sometimes some animals surface vertically from the water almost up to the flippers, remain in that position for about 0.5 min, then submerge without altering their upright posture. Some animals strike the water with their fins (Brown, 1961). This ability to assume a vertical position is taken advantage of in oceanariums. The pilot whale is gradually trained to rise higher and higher out of the water to reach food dangled above it. A large dolphin, such as the pilot whale, can thus be trained to leap clear of the water and even to "fly" above it (Fig. 305).

The extraordinary behavior of a herd of pilot whales once came to notice. This mixed herd consisted of about 150 pilot whales and small dolphins. Suddenly, some animals assumed a vertical position but with their head down (under the water) and each struck the water surface five or six times with its caudal flukes. They then assumed a horizontal position and rejoined the herd. Such a head-down position has been reported among pilot whales in other instances too (Brown, 1960).

Pilot whales are beached more often than other cetaceans, both individually as well as in groups. On October 7, 1948, as many as 46 pilot whales were cast ashore simultaneously on a beach in Florida; those found early in the morning, during low tide, were still alive. Four were transported by truck while the others perished on the coast in high tide (Obruchev, 1951). Beached groups usually consist of animals of various age but sometimes young ones exclusively.

A pilot whale in a Florida aquarium slept only at night in the first few months of captivity but later continued to sleep during the day also. While asleep, all of its body was submerged and only the dorsal fin and blowhole remained exposed above the water.

Pilot whales hear well under water and their aerial vision is excellent. In captivity, they invariably perceive the approach of the food attendant and swim immediately to the feeding place. One female pilot whale quickly learned to snatch food from the attendant's hand; it swam to the feeding site, stood vertical with its head above the water, and opened its mouth for the attendant to throw cephalopods inside. Washing of the

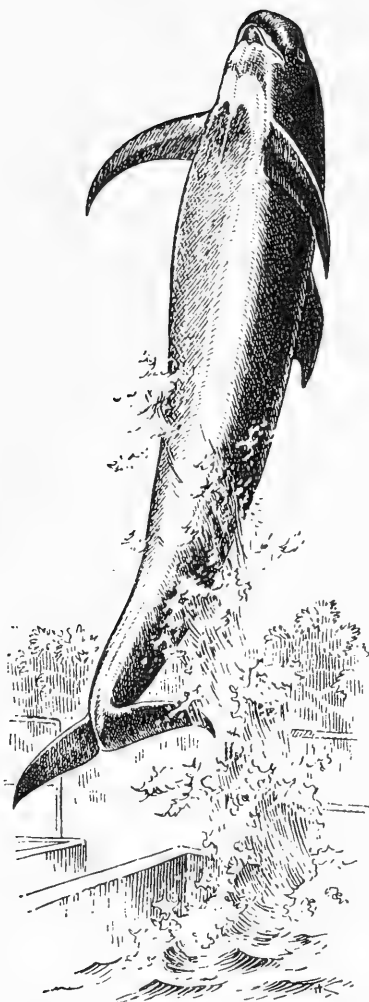


Fig. 305. Leaping pilot whale (figure by N.N. Kondakov).

pail signalled completion of feeding and the pilot whale would immediately swim away. A male loved to be combed with a brush and quickly approached anyone with a brush in his hand (Tomilin, 1957).

530 A pilot whale (body length 366 cm) caught on February 27, 1957 was housed in a tank 30.5 m long, 15 m wide, and 6.7 m deep. For the first few days the animal refused food and the attendant had to enter the tank in a diver's suit, open her mouth with metal tongs, and push squids inside which the whale gulped rapidly. After 10 days she began to swim to the wooden platform affixed to the side of the tank and to take

food from the tongs held by the attendant. The animal consumed more than 20 kg of squids per day. A large fish and two turtles were also kept in the same tank. During the feeding period sometimes the fish would snatch the squids from the tongs before the pilot whale and sometimes even snatched them from the whale's open mouth. This angered the pilot whale. She would stop feeding and chase the fish around the tank. The turtles also swam to the feeding platform, which irritated the whale. Once she threw herself on them with such vehemence that one suffered a broken shell. However, the pilot whale soon learned to avoid competition during feeding: she would stand vertically at the feeding platform with a third of her trunk projecting above the water, maintaining balance by slight movements of the caudal flukes, and thus receive the food high above the water surface.

This offered a basis for teaching the pilot whale various tricks. First, it was taught to leap clear of the water to reach food dangled high above its head and next to associate feeding with a whistle. This was followed by a "hand shake". As soon as the pilot whale appeared around the feeding platform, the trainer would clasp it around the flippers and whistle before feeding. Very soon the pilot whale began to anticipate the actions of the trainer. On hearing the whistle, it would turn on its side, "extend" the flippers to the trainer, then demand food. By the same method, it was taught to fetch a plastic dumbbell from inside the tank and eventually to "sing". At the command of the trainer, it would quiver its jaws and simultaneously blow air powerfully through the blowhole. The pilot whale learned these various tricks quite rapidly. It was not at all afraid of any unfamiliar object. When in the course of the experiments a large boat was dropped inside the tank, the whale exhibited no apprehension. To the contrary, after a few minutes it swam to the boat, fed tranquilly, and performed its tricks.

In the first week of February, 1958, the pilot whale lost its appetite. Next, it began to rub the genital slit against a stone or other projecting object at the bottom of the basin, including the diver's abandoned helmet. This behavior continued for nearly two weeks, after which the animal resumed normal feeding. Perhaps this was the period of its heat.

For a long time the pilot whale was friendly with the divers who entered the tank to feed the other animals, even attempting sometimes to snatch the food from their hands. But after nearly 14 months of living in the tank, it began to push the diver (or anyone entering the tank) with its head and to bite his hands while he was feeding the other animals. One diver barely escaped serious injury when, on the water surface, the pilot whale tried to pin him to the wall of the tank. Later, it chased three persons simultaneously, two of whom were photographers. It hit the leg

of one and zoomed to the second loudly clicking its teeth; all three made a hasty retreat. It then attacked the large photographic camera set up on a tripod at the bottom of the tank, hitting it with such force that the heavy lens was badly damaged. Four days later the pilot whale struck one of the divers so powerfully that he lost consciousness and barely escaped drowning. This change in the behavior of the pilot whale was attributed to its long lonely existence. In July, 1958, it was transferred to a basin with another small pilot whale and two blue-white dolphins. Initially the dolphins were frightened and shied away from the large pilot whale, but soon became emboldened and spent several hours nipping it behind the flippers whenever possible. This irritated the pilot whale who chased them but the more agile dolphins easily escaped. After about a month the animals became friends, swimming abreast, and often playing together. From the time the pilot whale began living with the other dolphins, its animosity against the divers ceased (Brown, 1960).

531

Migrations. Pilot whales probably perform seasonal migrations since they are more abundant in the North Atlantic Ocean (as in the Pacific Ocean also) in summer than in winter. Norwegian whalers hunting for small whales in the northwestern Atlantic catch the pilot whales mostly in the second half of summer. Thus in 1958, of the 216 pilot whales caught, 64 were bagged in July and 150 in August (Østby, 1959). Table 41 provides an idea of the duration of residence of pilot whales in the waters of Newfoundland.

In the first half of January, 1953, a large herd of pilot whales was sighted at 42° 30' N lat. and 52° W long.; evidently the effect of the Gulf Stream was more intense in the winter.

In the summer months, pilot whales regularly visit the large deep-water bays of Newfoundland and, concomitantly, though in small numbers, are found in the central part of the Labrador Sea. Similarly, pilot whales are regularly sighted in summer in the eastern waters of the North Atlantic, initially off the Faroe Islands and the southwestern coast of Norway, later off northwestern Norway, Iceland, and Jan Mayen Island, and at the end of summer, in the western part of the Barents Sea, in the waters of Medvezhii Island, and even at Spitsbergen.

Table 41. Observations on pilot whales in Newfoundland (Sergeant and Fisher, 1957)

Year	First observation	Subsequent observation
1953	July 8	November 4
1954	July 6	November 10
1955	July 15	October 22

The pilot whale is purportedly encountered in winter east of the Grand Bank south of Newfoundland in the waters of the North Atlantic current. Information on the migrations of the pilot whale in other regions of its range is so scant that no clear picture of migrations can be drawn. Apparently migrations are not very distinctly manifest since these animals are sighted in the northern as well as the southern part of the range throughout the year.

From 1926 through 1953 (July to October end), 20 instances of beached pilot whales were recorded on the coast of western Greenland, most of them in September. In the winter of 1931/32, a herd of pilot whales wintered on the coasts of western Greenland (Sergeant and Fisher, 1957).

Reproduction, growth, and development. The periods of mating and parturition in the pilot whale evidently last for about six months but most of the animals mate over a brief duration. The maximum number of matings presumably occurs in the spring months with parturition peaking in mid-August, although there have been instances of calves born from May through November. Stray cases of births have been recorded in almost all the months of the year. Gestation apparently continues for 15-15.5 months. As a rule, a single calf is born and twins are rare. There is a solitary record of a female with three embryos. The average length of male calves at birth is 178 cm, of female calves 174 cm. The teeth begin to cut at a body length of about 213 cm. This process ceases when the calf attains a length of about 274 cm. The growth of embryos and newborn pilot whales is shown in Table 42.

The calves begin independent feeding on squids at an average body length of 230 cm at the age of six- nine months; however, suckling does not cease and extends for about two years. Lactation of the female continues for 21-22 months. Instances of fresh impregnation during lactation are rare; the females usually ovulate at the end of lactation. Thus the full cycle of reproduction roughly covers 40 months. During the period of reproductive capability, the female produces, on average, nine calves.

532 Male calves record a much greater growth tempo than female calves. A young male living in a Florida aquarium added 30 cm to its length and put on 45 to 90 kg in four months. The average length of adult animals is usually about 396 cm. Females ovulate for the first time (attain sexual maturity) at six years of age at an average body length of 356 cm and males at the age of 12 years at an average body length of 490 cm. After attaining sexual maturity, the growth of the animal slows down. Males, which attain maturity later, are considerably larger than females. Most of the males in the group measured, fell in the 565-cm group and the maximum number of females in the 340-cm group. The maximum size

Table 42. Length and weight of embryos and calves of pilot whales (Sergeant, 1962b)

Embryos		Calves	
Length, cm	Weight, kg	Length, cm	Weight, kg
16.5	0.08	193	113.4
19.0	0.12	195	95.3
21.0	0.18	205	145.6
23.0	0.22	208	130.6
24.0	0.25	231	188.7
25.0	0.32	236	202.8
26.0	0.36		
31.0	0.54		
36.0	0.75		
41.0	1.16		
43.0	1.45		
48.0	1.54		
59.0	3.74		
114.0	21.00		
119.0	28.50		
165.0	60.00		

of the males was 617 cm and of the females 511 cm. The maximum recorded age of the males was roughly 40 years and of the females 50 years (Tomilin, 1957; Sergeant, 1959, 1962b).

Table 43 shows the composition of pilot whales caught in Newfoundland according to their sizes: the animals have been grouped into a series at 15-cm intervals. The total number of males measured was 1,275, of females 1,951 and the number falling in each length group is given. The data show that the size of adult males far exceeds that of adult females and that animals of all ages fall victim to the hunter.

533 Table 44 gives data on the age composition of the oldest groups of pilot whales caught and investigated. The age of the animals was determined from the tooth layers. From a sample of 518 pilot whales, males with a body length 549 cm and above (only 11 animals) and females with a body length 457 cm and above (22 animals) were taken. It can be seen from this Table that these animals were quite advanced in age, the females reaching a maximum age of 50 years.

Enemies, diseases, parasites, mortality, and competitors. As in the case of all other cetaceans, the killer whale is among the enemies of the pilot whale.

Bone tumors were detected among the diseases suffered by the pilot whale. The skin parasite *Isocyamus delphini* Guerin-Meneville was invariably detected around the mouth and in old wounds on the body of the Newfoundland pilot whale. *Conchoderma auritum* Linn. was detected on

Table 43. Size composition of pilot whales studied (Sergeant, 1962b)

Average length of animals in the group, cm	Number of animals in the group		Average length of animals in the group, cm	Number of animals in the group	
	Males	Females		Males	Females
168	6	10	396	59	169
183	15	22	411	41	259
198	12	17	427	61	278
213	20	16	442	44	221
229	13	12	457	36	170
244	28	32	472	36	50
259	51	48	488	37	10
274	54	61	503	37	5
290	63	66	518	41	—
305	52	78	533	67	—
320	61	83	549	76	—
335	59	83	564	84	—
351	53	59	579	47	—
366	60	73	594	23	—
381	33	129	610	6	—

Table 44. Age of the largest pilot whales from a sample of 518 animals (Sergeant, 1962b)

Age, years	Number of animals	
	Males	Females
21-25	4	2
26-30	2	6
31-35	3	8
36-40	2	3
41-45	—	2
46-50	—	1
Total	11	22

the gums and teeth, and *Cyanus globicipitis* Lütken, *Xenobalanus globicipitis* Steenstrup, and *Cyrolama globicipitis* van Beneden on the body.

Eight species of endoparasites have been recorded: trematodes one, cestodes three, nematodes three, and acanthocephalans one. The trematode *Campula gondo* Yamaguti was found only in the bile ducts of the pilot whale from the Pacific Ocean. The cestode *Trigonocotyle lintoni* Guiart, parasitizing the intestine, is likewise known only in pilot whales from the Atlantic Ocean and the Mediterranean Sea. *Phyllobothrium delphini* Bosc, widely distributed among marine mammals, parasitizes the skin. In addition to the pilot whale, it has been detected in six other

species of toothed whales, in right whales, and in Weddell's seal from the Atlantic and Pacific oceans, the Mediterranean Sea, and Antarctic waters. The cestode *Monorygma grimaldi* Monier is a parasite in the abdominal cavity, mesentery, and diaphragm of pilot whales and three other species of dolphins of the Atlantic Ocean and the Mediterranean Sea. The nematode *Anisakis (Anisakis) typica* Diesing localizes in the stomach of the pilot whale and three other species of dolphins; it has been found in the North Sea and on the coasts of southeastern Africa. The nematode *Stenurus globicephale* Baylis and Daune, parasitizing in the blowhole, bronchi, and the circulatory system, has been reported only in the pilot whale from the North Atlantic. The nematode *Torynurus convolutus* Kühn parasitizes the bronchi and blood vessels of the lungs of the pilot whale and also common porpoises and one more dolphin (species not established). It has been detected in the waters of Europe, the North Atlantic, Sakhalin, and the Sea of Okhotsk. The only species of acanthocephalans, *Bolbosoma capitatum* Linstow, localizes in the intestine of the pilot whale, sperm whales, and false killer whales from the Atlantic Ocean and the Mediterranean Sea (Delamure, 1955).

Field characteristics. This species differs from other dolphins in having a round head which projects high above the water, a dorsal fin with a very broad base and its apex turned posteriorly, and slower movements. (V.A.)

Economic Importance

The pilot whale is hunted in Newfoundland and the Faroe Islands by Norwegian ships operating close to Norway as well as in the North and Barents seas, in addition to other species of small cetaceans; it is also hunted in the waters of Japan (Table 45).

534 A relatively large number of pilot whales is caught only in Newfoundland and in the Faroe Islands; these animals are of considerable local importance. In all other waters, their catch is too small to be significant.

Hunting is done by various methods. In Norway and Japan, in addition to other species of small whales (Minke whale, killer whale, beaked dolphins, etc.), they are shot with small-bore harpoon guns from small boats. In Newfoundland, most of the pilot whales are caught by chasing large herds into shallow bays of islands and harpoons used to a lesser extent.

The flesh of the animals caught is used as food (in Japan) and also as feed for fur-bearing animals in farms (Newfoundland). Oil is obtained from blubber. (V.A.)

Table 45. World catch of pilot whales (international whaling statistics)

Year	Newfoundland	Faroe Islands	Norway	Japan
1950	172		10	
1951	3,100		8	
1952	3,155		2	
1953	3,584		1	
1954	2,298			
1955	6,612		13	61
1956	9,799		1	279
1957	7,797		80	174
1958	789		216	197
1959	1,725	1,422	224	144
1960	1,957	1,680	331	168
1961	6,262	1,892	295	133
1962	150	1,753	43	80
1963	221	2,194	71	228
1964	2,849	1,386	54	217
1965	1,520	1,599	32	288
1966	887	1,488	339	199
1967	739	1,979	117	237
1968	204	1,749	31	166

Genus of Pygmy Killer Whales

Genus *Feresa* Gray, 1870

1870. *Feresa*. Gray. Proc. Zool. Soc. London, p. 77. *Orca intermedia* Gray
= *Feresa attenuata* Gray. (V.H.)

Small dolphins, with a body length up to 244 cm.

The head is rounded and has no "beak". The dorsal fin is quite high.

The main body color is dark gray.

The rostrum occupies nearly one-half of the skull length. The anterior part of the premaxillae is flattened; their inner edges are set off from each other. The lower jaw has a keel in the zone of the symphysis. Teeth $\frac{10-11}{11-13}$. Vertebrae 68-71.

Biology has not been studied. These dolphins apparently feed on squids and fish.

There is very little information on the sites where this rare dolphin is found: in the North Pacific Ocean from Alaska to Guatemala in the east, on the coasts of Japan, in the Yangtze estuary, and on the coasts of China in the west.

This dolphin has not been reported in the USSR but it might occur in the waters of Kuril Islands and in the Sea of Japan. (V.S.)

PYGMY KILLER WHALE

Feresa attenuata Gray, 1875

1827. *Delphinus intermedius*. Gray. Philos. Mag. or Annals, 2, p. 376.
Type locality not established. Nom. praeocc.

1875. *Feresa attenuata*. Gray. Journ. Mus. Godeffroy (Hamburg), 8,
p. 184.

1856. *Feresa occuleta*. Jones and Packard. Proc. Biol. Soc., Washington,
69, p. 167. Substituted for *Delphinus intermedius* Gray. (V.H.)

Only species of the genus.

Somewhat resembles the false killer whale. The body is elongated and spindle-shaped. The head is relatively small. The highly developed adipose pad [melon] projects anteriorly to impart a circular feature to the head (Fig. 306). The flippers are crescent-shaped, quite broad at the base and pointed at the tips. The height of the dorsal fin is slightly less than its basal length. It is arcuately notched along the posterior margin. The caudal flukes are relatively small.

The body is a monochromatic dark gray. The margins of the jaws and the region around the anal opening are white. An anchor-shaped light-colored patch is seen on the breast. Wavy pale-colored bands run on the flanks (Nishiwaki, 1966).

The skull (Fig. 307) is highly shortened and measures about 16% of the body length. The short rostrum, broad at the base, gradually, but not very significantly, narrows toward the tip. The upper side of the rostrum is slightly concave (Yamada, 1954). The teeth are fairly large with crowns about 1 cm high. Cervical vertebrae 7, thoracic 12-13, lumbar 16-17, and caudal 32-34.

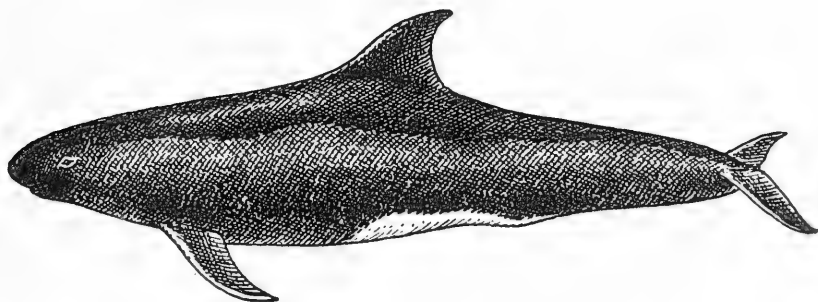


Fig. 306. Pygmy killer whale, *Feresa attenuata* (figure by N.N. Kondakov).

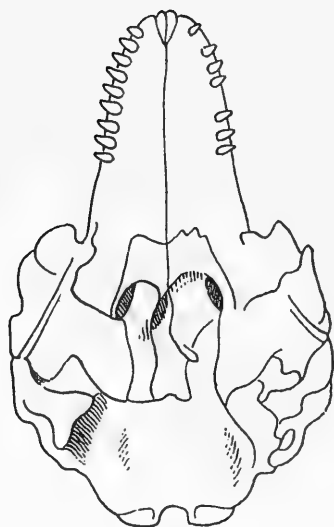


Fig. 307. Skull of the Pygmy killer whale, *Feresa attenuata* (figure by N.N. Kondakov).

The body length of males (Japan; Nishiwaki, 1966) ranges from 214-244 cm, of females 208-227 cm. The maximum weight recorded was 225 kg for a male measuring 244 cm in length. The body proportions of males with a body length of 214-244 cm and of females with a body length of 208-227 cm respectively (as percentage of body length) are: from tip of snout to blowhole 6.8-11.9 and 7.2-11.1, to flippers 16.7-21.6 and 18.5-22.4; from notch between caudal flukes to anal opening 34.2-37.2 and 34.2-38.6; length of flippers 18.3-22.1 and 14.7-22.2, maximum width of flippers 6.1-6.7 and 5.8-7.0; length of base of dorsal fin 12.6-15.4 and 14.0-16.6, height of dorsal fin 9.4-11.6 and 9.6-10.9; and spread of caudal flukes from apex to apex 23.8-27.3 and 23.0-28.4.

The measurements of 14 skulls (Japan; Nishiwaki, 1966) with a condylobasal length of 356 to 390 mm (as percentage of this length) are: length of rostrum 44.7-49.2, basal width of rostrum 27.7-31.8, interorbital width 53.7-60.7, length of lower jaw 72.2-79.9, and length of mandibular symphysis 8.7-10.1.

536 Information on the geographic distribution of this species is very scant, with only a few recorded finds and observations (Fig. 308). It has been noticed in the waters of Senegal and in the North Atlantic. It is known in the Yangtze estuary, along the coasts of Honshu Island, and in the North Pacific Ocean. (V.S.)

Biology has not been studied.

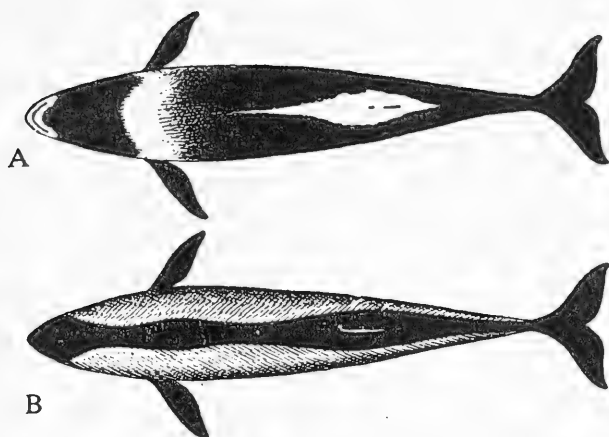


Fig. 308. Pygmy killer whale, *Feresa attenuata* (figure by N.N. Kondakov).
A—coloration of underside; B—of upper side.

Genus of Common Porpoises

Genus *Phocoena* G. Cuvier, 1817

1817. *Phocoena*. G. Cuvier. Règne Animal, ed. I, I, p. 279. *Delphinus phocoena* Linnaeus, 1758.

1828. *Phocoena*. Gray. Spicil. Zoologica, I, p. 2. *Delphinus phocoena* Linnaeus, 1758. (V.H.)

Small dolphins, with a maximum body length of 2 m.

These dolphins have no “beak”. The head is obtuse and the forehead flattened. The anterior margin of the low dorsal fin, short flippers, and caudal flukes bears small horny tubercles (sometimes these are present only on the dorsal fin).

The body is dorsally dark, gradually turning white on the ventral surface.

The rostrum of the skull is equal to or slightly shorter than the cranium. The posterior section of the premaxillae anterior to the bony nares forms a prominence. The pterygoid bones are separated by a gap. The boundaries of the interparietal bones are invariably very prominent.

Teeth $\frac{16-30}{16-27}$. They have a slightly flattened crown and are set off from the root by a neck. Vertebrae 62-66. Ribs 12-14 pairs. The sternum is non-segmented. Phalangeal formula: I_1-3 , II_5-10 , III_5-8 , IV_2-6 , and V_1-3 .

These dolphins are ichthyophagous, surviving mainly on benthic fish (benthichthyophagous). The females whelp every year. Gestation extends for nine to ten months and lactation for about four months.

Females are ready for fertilization two to three months after parturition, while still nursing a calf.

Common porpoises are distributed in the North Atlantic from the Barents Sea and Davis Strait to New Jersey in the west and the Mediterranean, Black, and Azov seas, and Senegal waters; in the South Atlantic from Rio de la Plata (35° S lat.) to Cape Horn and South Georgia; in 538 the North Pacific Ocean, from the Chukchi Sea to Mexico in the east and Japan in the west; in the South Pacific Ocean, from Paita in Peru (5° S lat.) to Cape Horn (Hershkovitz, 1966) (Fig. 309).

The members of this genus are thus absent in the Indian Ocean, in the western part of the South Pacific Ocean, and in some tropical and equatorial parts of the Atlantic and Pacific oceans.

The genus comprises four species: 1) *P. phocoena* Linnaeus, 1758; 2) *P. dioptrica* Lahille, 1893; 3) *P. spinnipinnis* Burmeister, 1865; and 4) *P. sinus* Norris and McFarlan, 1958. Sometimes the genus is divided into a larger number of species.

Only one species is encountered in the USSR waters: the common porpoise, *P. phocoena* Linnaeus, 1758.

The common porpoises are presently not of commercial importance. (V.S.)

COMMON PORPOISE¹⁵

Phocoena phocoena Linnaeus, 1758

1758. *Delphinus phocoena*. Linnaeus. Syst. Nat., I, p. 77. Baltic Sea ("Oceano Europeo Balthico")
1827. *Phocoena communis*. Lesson. Man. Mammal, p. 413. Renamed as *Delphinus phocoena* auct.
1865. *Phocoena vomerina*. Gill. Proc. Ac. Nat. Sc. Philadelphia, 17, p. 178. Puget Sound, Washington State.
1905. *Phocoena relicta*. Abel. Jahrb. K.K. Geol. Reichsanstalt, Wien, 55, p. 387. Crimean waters of the Black Sea. (V.H.)

Diagnosis

Only species of the genus encountered in the USSR.

Description

The external appearance of the common porpoise is typical: the body build is much heavier than that of dolphins, somewhat stunted, and the

¹⁵ Also locally known as "Azovka," "Pykhtun," "Svinka" [porpoise], etc. (Black Sea).

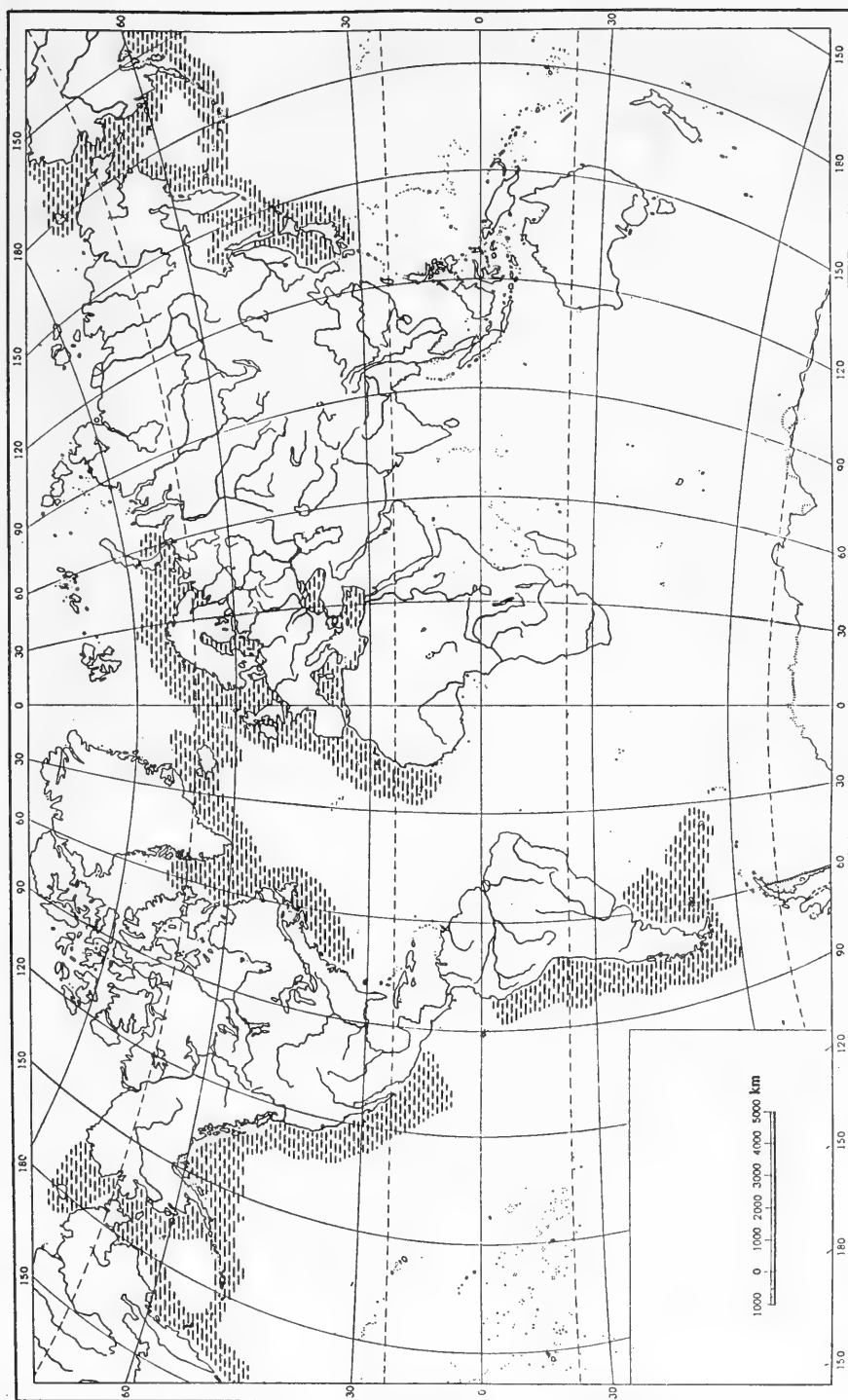
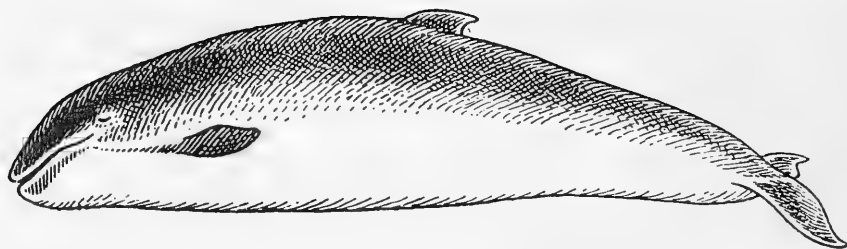


Fig. 309. Range of the genus of common porpoises, *Phocoena* (V.A. Arsen'ev).



539 Fig. 310. Common porpoise, *Phocoena phocoena* (figure by N.N. Kondakov).

trunk thickset. The head is short. The flippers are oval and the dorsal fins triangular (Fig. 310).

Horny tubercles 12-16, less frequently 18-20, occur along the anterior margin of the dorsal fin in common porpoises (adult animals and embryos) of the Black and Azov seas (Tsalkin, 1938b). It has been suggested that these tubercles represent derivatives of the thick skin cover (Kükenthal, 1889-1893). Two or three hairs are seen on each side of the snout in embryos. The color of the dorsal surface varies from a dark gray to almost black. The light-colored abdomen is sometimes sharply demarcated from the dark dorsum but sometimes the transition in coloration is altogether imperceptible (Tsalkin, 1938b). A faintly perceptible dark gray band runs from the zone of the ear openings toward the navel on each side of the body, while another almost black band extends from the corner of the mouth to the base of each flipper (Barabash-Nikiforov, 1940). Instances of partial or total albinism are encountered occasionally.

The form of the tooth crown is variable—from almost conical to a form with three faintly discernible cusps. The anterior surface of the crown is slightly turned inside the cavity. When the mouth is closed, the teeth on the lower jaw fall inward of the upper teeth. Among the Black and Azov sea common porpoises, the number of teeth in the upper jaw varies from 44 to 60 (more often, 54) and in the lower jaw 38 to 55 (more often, 44-46) (Tsalkin, 1938b). The teeth of this common porpoise are characterized by curvature, distortion of the roots, and thickening in the lower portions (Tsalkin, 1938; Barabash-Nikiforov, 1940). As age advances, the teeth may wear down or even drop out. Cervical vertebrae 7, thoracic 12-14, lumbar 14-17, and caudal 27-32. The sections of the vertebral column comprise (as percentage of its length): cervical 1.9-3, thoracic 22.1-24.6, lumbar 30-34.2, and caudal 40-44 (Tomilin, 1957). Six to eight pairs of ribs are articulated with the sternum in the embryos and usually five pairs in adults.

Females are slightly larger than males. The difference in body length between mature females and males from the Black and Azov seas averages 7 cm (Tsalkin, 1938).

The main body measurements of this species of common porpoises (eight animals) from the Black Sea average (Tsalkin, 1938) (in cm): body length 163; distance from tip of snout to base of flippers 32, to anterior margin of dorsal fin 73; and length of flippers 22. The length of the largest common porpoises from the Black and Azov seas is (in cm): male 167 and female 180; from the North Pacific Ocean: female 178.5; and from the North Atlantic: male 186.

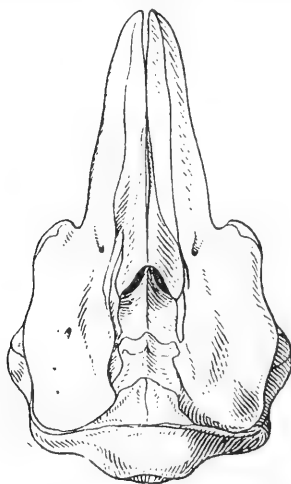
The average main skull measurements (measurements of five males and three females; Tomilin, 1957) (Fig. 311) are respectively (in cm): condylobasal length 25 and 27, length of rostrum 11 and 12, width of rostrum at base 7 and 8, and length of lower jaw 19 and 21. (V.S.)

Geographic Distribution

Temperate and partly cold waters of the North Atlantic and the North Pacific oceans; predominantly the coastal zone.

Geographic Range in the USSR

In the basin of the Atlantic Ocean, this porpoise is commonly encountered in the Barents Sea where it reaches the coasts of Novaya Zemlya and Yugorsk Shar and is abundant on the Murman coast; it is also common in the White Sea (waters of Kanin, Letn'aya and Tersk



539 Fig. 311. Skull of the common porpoise, *Phocoena phocoena* (figure by N.N. Kondakov).

coasts, and Gulf of Kandalaksh), Kara Sea (transgresses into its western section), Baltic Sea, and almost the entire coastal water body of the Black and Azov seas (Fig. 312).

In our waters of the Pacific Basin, it is common in the Sea of Japan and the Sea of Okhotsk, on both sides of the Kuril range, along the coasts of Kamchatka, Koryatsk land, and the Gulf of Anadyr, around the Commander Islands in the Bering Sea, in the Bering Strait, and in the Chukchi Sea where it penetrates north of 70° N lat. (east of Point Barrow, 71°24' N lat.). Its range in the west is not known.

Geographic Range outside the USSR

In the western part of the North Atlantic, the common porpoise is known from New Jersey (39° N lat.), and possibly more southward, up to Davis Strait, Baffin Bay, and coasts of Greenland in the eastern part of the Atlantic Ocean, from the waters of Senegal and Dakar in northern Africa (about 15° N lat.) to the Barents Sea, Iceland, and east coast of Greenland (Scoresby Sound), i.e., roughly up to 70° N lat. The range covers the entire Baltic Sea. Transgressions into the Mediterranean Sea from the Black Sea as well as from the Atlantic Ocean are known (Fig. 313).

In the Pacific Ocean, this species lives along the eastern coasts of the Korean peninsula and in the waters of Japan. It inhabits the entire coastal waters of the American continent down to California and Mexico from the Chukchi Sea (Point Barrow) and the Bering Sea, including the coastal waters of the Aleutian Islands (Kleinenberg, 1956a; Tomilin, 1957; Hall and Kelson, 1959; Nishiwaki, 1966). (V.A.)

Geographic Variation

In the Northern hemisphere, the species forms three subspecies that are almost indistinguishable although geographically disjointed. All the three subspecies are encountered in the waters of the USSR.

1. **Northern Atlantic common porpoise**, *P. p. phocoena* L., 1758 (syn. *communis*). This is the largest of the subspecies with a body length up to 186 cm, condylobasal length of skull 255-259 mm, width of condyle 65-71 mm, and height of occipital condyle 38-42 mm. The rostrum is hardly shortened. Tubercles are seen on the anterior margins of the flippers, dorsal fin, and caudal flukes.

This subspecies is encountered in the Barents, White, Kara, and Baltic seas.

Outside the USSR, it has been reported in the waters of the North Atlantic Ocean.

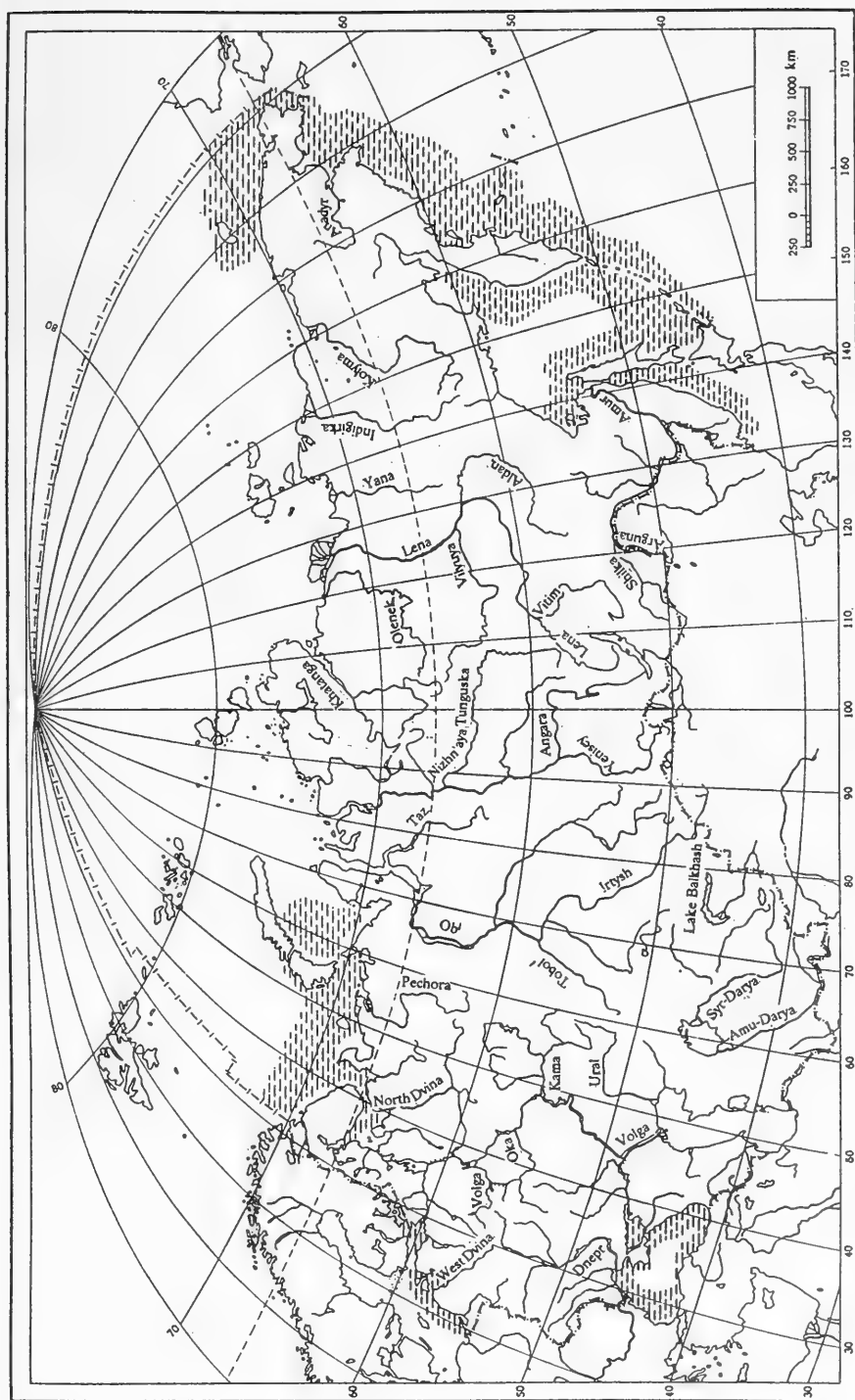


Fig. 312. Range of the common porpoise, *Phocoena phocaena*, in the USSR (V.A. Arsen'ev).

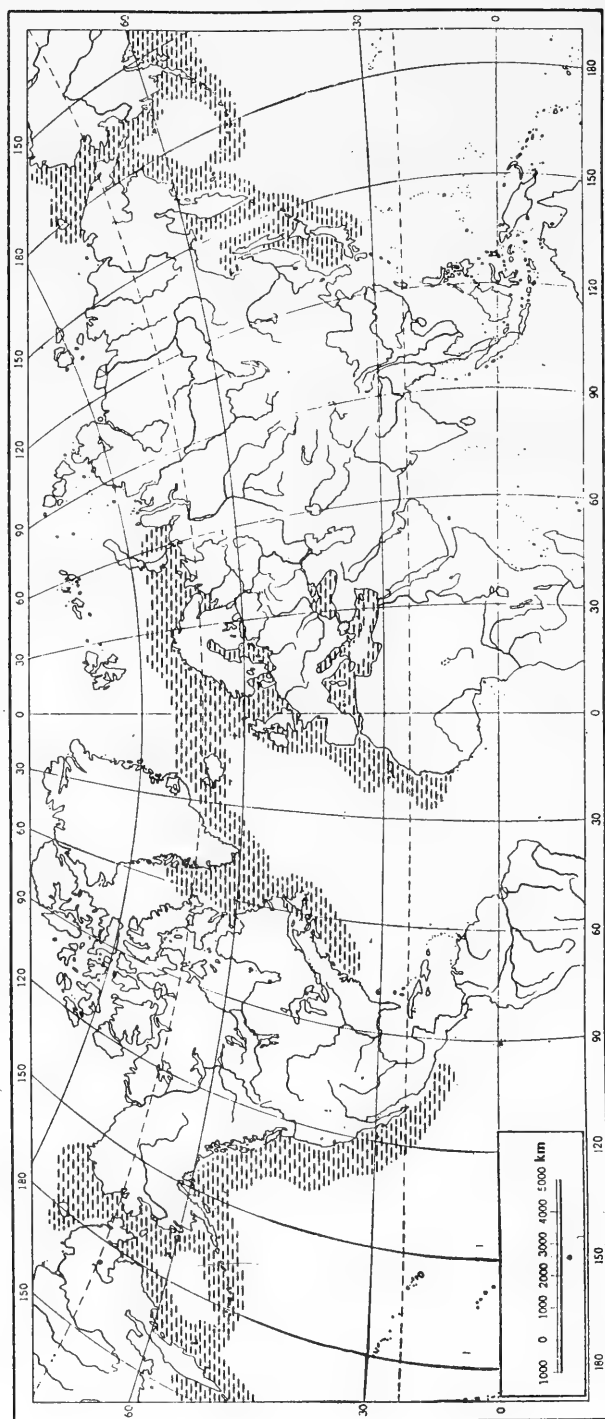


Fig. 313. Species range of the common porpoise, *Phocoena phocoena* (V.A. Arsen'ev).

2. **Black Sea common porpoise**, *P. p. relicta* Abel, 1905. This form is of medium dimensions, with a body length up to 180 cm, condylobasal length of skull in males 245-255 mm, in females 269-274 mm; width of condyle in males 54-62 mm, in females 58-63 mm; height of occipital condyle in males 32-36 mm, in females 37-39 mm. The tubercles on the anterior margin of the fins are totally reduced.

This subspecies is encountered in the Black and Azov seas.

Outside the USSR, transgressions have been reported for the Marmora and Mediterranean seas.

3. **Pacific common porpoise**, *P. p. vomerina* Gill, 1865. This is the smallest of the subspecies with a body length up to 178 cm, condylobasal length of skull 258-293 mm, width of condyle 68-70 mm, and height of occipital condyle 40-43 mm. The rostrum is highly elongated.

This subspecies is encountered in the Chukchi, Bering, Okhotsk, and Japan seas, and in the waters of Kuril Islands from the Pacific Ocean side.

Outside the USSR, it has been reported in the American waters of the Pacific Ocean from the Chukchi Sea to the Mexican coasts and in the waters of Japan. (V.A.)

Biology

Population. The species can be regarded as relatively abundant. The least populous of the three subspecies is the Azov-Black Sea common porpoise, which is confined to an extremely restricted range. Populations of the other two subspecies occupy extensive water bodies in which they are commonly encountered and are perhaps quite abundant.

Food. Information on the food of the Atlantic and Pacific populations is extremely scant while that on the food of the Black Sea population is more widely available (Table 46).

543 Two species of pelagic fish, viz., smelt (49.5%) and Black Sea anchovy (18.5%), occupy the primary position in terms of the quantum of fish found in the stomach of the Azov-Black Sea common porpoise. All the species of goby (bottom-dwelling fish) comprise only 30.9%. The rest of the species of fish in the food of the common porpoise constitute only a few tenths of one per cent. In terms of the number of fish objects encountered, pelagic fish comprise 68.8% and benthic fish 31.2%. However, in terms of weight (as percentage of total weight of food), rotan goby occupies the first position (32.4%), followed by round goby (31.2%), smelt (14.5%), and Black Sea anchovy (11.0%). Thus, the group of benthic fish constitutes 67.9% of the total weight of food intake and the group of pelagic fish 32.1%

Table 46. Food objects of the common porpoise

Azov-Black Sea (Tsalkin, 1940)	North Atlantic (Tomilin, 1957, 1962)	North Pacific (Sleptsov, 1955; Tomilin, 1957)
Fish	Fish	Fish
Round goby, <i>Gobius melanostomus</i>	Cod, <i>Gadus morhua</i>	Pacific cod, <i>Gadus morhua macrocephalus</i>
Rotan goby, <i>G. rotan</i>	Capelin, <i>Mallotus villosus</i>	Capelin, <i>Mallotus villosus</i>
Mushroom goby, <i>G. cephalarges</i>	Navaga, <i>Eleginus navaga</i>	Pacific navaga (saffron cod), <i>Eleginus gracilis</i>
Syrman goby, <i>G. syrman</i>	Sand eel, <i>Ammodytes hexapterus</i>	Polar cod, <i>Boreogadus saida</i>
Toad goby, <i>Mesogobius batrachocephalus</i>	Whiting, <i>Odontogadus merlangus</i>	Herring, <i>Clupea harengus</i>
Black Sea flounder, <i>Pleuronectes flesus luscus</i>	Common mackerel, <i>Scomber scombrus</i>	Shad, <i>Alosa sapidissima</i>
Black Sea sole, <i>Solea nasuta</i>	Pollock, <i>Pollachius virens</i>	Shark, <i>Squalus</i> sp. (?)
Black Sea anchovy, <i>Engraulis encrasicolus</i>	Herring, <i>Clupea harengus</i>	Sablefish (black cod), <i>Anoplopoma fimbria</i>
Black Sea silverside-smelt, <i>Atherina pontica</i>	Sardine, <i>Sardina</i> sp.	Whitefish (<i>Leucichthys</i>)
Perch, <i>Lucioperca lucioperca</i>	Sole, <i>Solea</i> sp.	Crustaceans
Bream, <i>Abramis brama</i>	Eel, <i>Anguilla anguilla</i>	Shrimps
Golden gray mullet, <i>Mugil auratus</i>	Salmon (small)	Mollusks
Black Sea whiting (haddock), <i>Gadus euxinus</i>	Sprat, <i>Sprattus</i> [= <i>clupea</i>]	Cephalopods
Black Sea shad (herring), <i>Caspialosa</i> sp.	<i>sprattus</i>	
	Trout	
Crustaceans	Crustaceans	
<i>Balanus improvisus</i>	Decapods	
<i>Brachinotus lucasii</i>	Mollusks	
<i>Idothea baltica</i>	Cephalopods (<i>Loligo pealittii</i>)	
<i>Leander</i> sp.	Algae	
Mollusks		
Algae		
<i>Ulva lactuca</i>		

Most mollusks probably enter the stomach of porpoises through the fish they consume. Two species of crustaceans (*Idothea baltica* and *Leander* sp.) can be regarded as incidental food objects as they were found in only two stomachs. Alga was found in the three groups of porpoise in large quantities and probably serves as food.

Thus, fish represent the almost lone source of food to the Azov-Black Sea common porpoise; most of them are benthic and a small percentage

pelagic. The latter serve as the main food only in the period of massive migrations (Black Sea anchovy) when they form concentrations of large proportions.

Seasonal variations in food types have been noticed: benthic fish predominate in winter, while in summer Black Sea anchovy and smelt play an extremely important role in the food of common porpoises during the period of migrations of these fish from the Black Sea into the Azov Sea and back in spring and autumn (Tsalkin, 1940).

544 The North Atlantic porpoises feed mainly on fish (benthic as well as pelagic forms). Cephalopods and other mollusks, crustaceans, and algae play no significant role in their food. The nature of the food of the Pacific porpoises is very similar to that of the other populations.

Daily activity and behavior. The porpoises of the Azov-Black Sea populations (probably the others too) avoid the open seas and are encountered more in the coastal shallow waters (Fig. 314). They are usually confined to small groups of not more than 10 animals. Relatively larger groups are encountered only in the period of massive migrations of fish which serve as their food. Exhalation and inhalation occur at not more than 30-sec intervals although instances of porpoises remaining submerged for 6 min are known. Their movement is comparatively slow. Intense flexure of the body while diving is a characteristic feature. The porpoises of this species, with rare exception, do not trail behind moving ships.

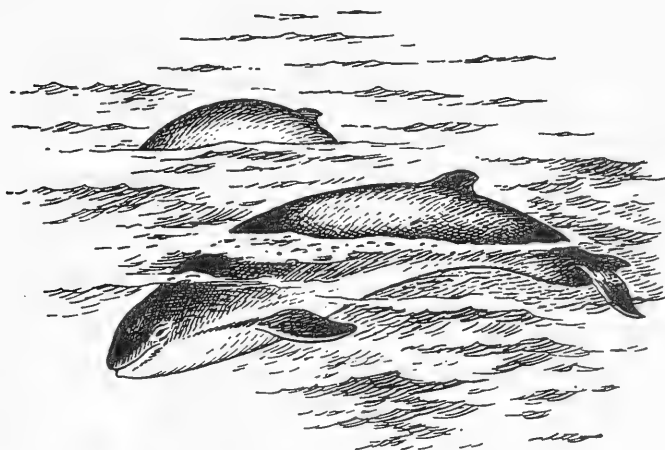


Fig. 314. Common porpoises at sea (figure by N.N. Kondakov).

Instances of the transgression of porpoises into rivers are not rare. They have been noticed not only in the Black Sea rivers (Don and Danube), but also in the Thames, Seine, Rhine, Elba, Neva, and other rivers. Sometimes the animals advance up the river for hundreds of kilometers from the estuary (Kleinenberg, 1956a; Tomilin, 1957, 1962).

Seasonal migrations and transgressions. The migrations of common porpoises have not been studied although some seasonal migrations undoubtedly do occur. It is quite obvious that these porpoises spend only the summer months in the northern parts of the range of the Atlantic and Pacific oceans but abandon these waters in winter. The southward movement of these porpoises into the Baltic Sea is quite impressive. Short seasonal migrations have been observed in the Black Sea in which the animals spend the winter; in spring, they are seen in the Azov Sea but return again to the Black Sea for winter.

The rare departures of common porpoises from the Black Sea into the Sea of Marmora and even into the Mediterranean Sea, their transgressions into the Mediterranean Sea from the Atlantic Ocean, and their passage in the easternmost part of the Baltic Sea (Kronshtadt) and through Neva even into Lake Ladoga, can be regarded as unusual transgressions.

Reproduction, growth, and development. Data on reproduction biology are available mostly for the Azov-Black Sea populations but these can be extrapolated to the other two populations with sufficient justification.

The periods of mating and parturition, although quite protracted, occur predominantly in the summer months. The Black Sea common porpoise mates from the end of June to October with a peak in August. The duration of gestation has been put at 9-10 months. Births occur from April to July. Most females whelp in May-June (Tsalkin, 1940). In the Baltic Sea, mating peaks in July and August while the largest number of calves are born in May and June. The growth rate of the embryo is quite high (Table 47). The embryos of common porpoises (Fig. 315) from the Baltic sea recorded an average weight increment of 5 g per day (total 160 g) in the one-month period from November 15 through December 15, 11 g per day (total 340 g) from December 15 through January 15, and 30 g per day (total 920 g) from January 15 through February 15.

Usually a single large calf (twins are very rare) measuring half the length of the mother's body, sometimes even longer, is delivered. The average length of a newborn calf is 75 cm (63-86 cm) and it weighs 2.8-7.9 kg. Lactation extends for about four months. The composition of the milk of the Azov-Black Sea common porpoise is as follows (%): fat 33.9, protein 5.22, sugar 1.28, dry residue 7.1, ash 0.6, and water 59.0 (Ural'skaya, 1957). In some cases, the milk may contain up to 45.8% fat.

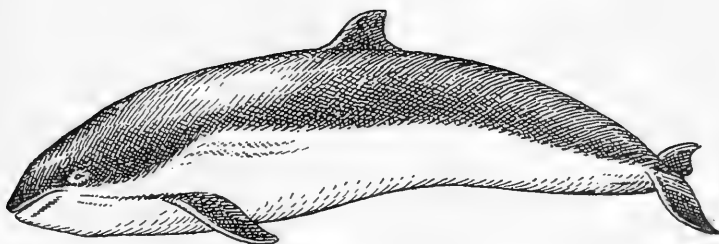


Fig. 315. Embryo of the common porpoise (figure by N.N. Kondakov).

Table 47. Monthwise dimensions of embryos, mm (Tomilin, 1957)

Month	Azov-Black Sea basin				North Atlantic Ocean and Baltic Sea				North Pacific Ocean			
	Number of animals	Mean	Min.	Max.	Number of animals	Mean	Min.	Max.	Number of animals	Mean	Min.	Max.
July	—	—	—	—	1	600	—	—	—	—	—	—
Aug.	2	30	10	50	—	—	—	—	—	—	—	—
Sept.	8	60	10	130	—	—	—	—	—	—	—	—
Oct.	67	120	50	200	1	190	—	—	—	—	—	—
Nov.	33	190	80	240	6	176	92	240	—	—	—	—
Dec.	4	250	120	300	46	232	148	318	—	—	—	—
Jan.	6	320	190	380	47	296	225	380	2	248	239	258
Feb.	—	—	—	—	23	356	250	450	2	397	384	411
March	263	460	210	610	2	535	520	550	1	486	—	—
April	28	580	370	820	5	650	590	740	2	495	480	510
May	35	730	620	840	2	675	610	740	1	660	—	—
June	7	820	780	850	1	710	—	—	—	—	—	—
Total	453		10	850	134		92	740	8		239	510

The calf is capable of swimming and accompanying the mother immediately after birth. The male to female ratio among newborn calves is close to one.

546 At a body length of 130-145 cm, many females of the Black Sea common porpoise are still immature. More than half the females (59%) with a body length of 145-150 cm and 79-100% of females 150 cm or longer were gestating. The smallest gestating female among the Black Sea common porpoises was 130 cm long and among the Baltic Sea animals 136 cm (weight 50 kg) (Tomilin, 1962).

Enemies, diseases, parasites, mortality, and competitors. In oceanic waters the killer whale represents the most dangerous enemy of the common porpoise, which is a food item for the former. It is possible that the

porpoise may fall prey to large sharks. Apart from bone tumors, no other diseases have been reported for these porpoises. Very severe infection with helminths could be the cause of death in some cases. Among all the cetaceans, the common porpoise is one of the primary hosts for a large number of helminths.

Eighteen species of helminths have been registered in the common porpoise: trematodes four, cestodes three, nematodes nine, and acanthocephalans two.

Two species of trematodes have been reported exclusively in common porpoises. *Campula oblonga* Cobbold, parasitizing the bile ducts of the liver, was detected in the European and American waters of the North Atlantic. *Pholeter gastrophilus* Kossack, parasitizing the mucous membrane of the pyloric section of the stomach, was found among dolphins caught in Baltiisk port. The trematode *Distomum philocholum* Creplin, localizing in the liver, has been encountered in white-sided dolphins in European waters as well as in common porpoises. This species parasitizes the bile ducts of the liver of common porpoises and three species of pinnipeds in the Atlantic and northern Arctic oceans; it is also known in three species of land carnivores.

The three species of cestodes belong to the genus *Diphyllobothrium*. Of these, *D. stemmacephalum* Cobbold was found in the small intestine of only common porpoises (North Atlantic and Black Sea on the Rumanian coasts); *D. lanceolatum* Krabbe parasitizes the intestine of common porpoises and four species of seals (North Atlantic and Pacific oceans); *D. latum* L., apart from common porpoise, is found in six species of pinnipeds, several species of land carnivores, domestic animals, and man; it has been detected among marine animals in the North Atlantic and northern Arctic oceans.

Anisakis (Anisakis) simplex Rudolphi, a nematode of common porpoises, is very widely distributed among marine mammals (parasite of the gullet, stomach, and intestine) and has been found in ten species of toothed whales, two species of baleen whales, and in Steller's sea lion in the North Sea and in the Pacific Ocean (Kamchatka, Japan, and New Zealand). *Anisakis (Anisakis) typica* Diesing, in addition to common porpoises, is a parasite of the stomach of three species of dolphins from the North Sea and waters of South Africa in the Atlantic Ocean. *Terranova (Terranova) decipiens* Krabbe, apart from common porpoises, has been reported among many species of marine mammals (17 species and subspecies of pinnipeds, 2 species of baleen whales, and 1 species of dolphins) and localizes in the stomach and intestine; it has been detected in the basin of the northern Arctic, Atlantic, and Pacific oceans, and around Antarctica. The nematode *Pseudalius inflexus* Rudolphi has been found

in the bronchi, blood vessels, and heart only of common porpoises from the North Atlantic coasts of Europe and the Asian coasts of the Pacific Ocean (not recorded in USSR waters). Of the three species of the genus *Halocerus*, *Halocerus (Prohalocerus) invaginatus* Quekett has been found in the lungs of only common porpoises from the waters of California, the Baltic Sea, and the Atlantic Ocean (not found in USSR waters). *Halocerus (Posthalocerus) taurica* Delamure and Skrjabin and *H. (Posthalocerus) ponticus* Delamure parasitize the lungs of only the Azov-Black Sea common porpoise. *Stenurus minor* Kühn, aside from Azov-Black Sea and Atlantic common porpoises, has been found in belugas in the northern Arctic Ocean, North Atlantic Ocean, North Sea, on the Asian coasts of the Pacific Ocean, and in the Black and Azov seas. It localizes in the bronchi, heart, blood vessels, and auditory organs. It is possible that the large number of the nematode *Stenurus minor* encountered in all the

547 Azov Sea porpoises may cause deafness in them. *Tozynurus convolutus* Kühn, parasitizing the bronchi and blood vessels of the lungs of animals in the European waters of the North Atlantic and coasts of Sakhalin in the Pacific Ocean, has been detected in pilot whales as well as common porpoises.

The acanthocephalans *Corynosoma semerme* Forssell and *Corynosoma strumosum* Rudolphi parasitize the intestine. The former is known in common porpoises, 6 species of pinnipeds, and 6 species of sea birds; the latter in common porpoises, 11 species of pinnipeds, belugas, 10 species of birds, and in cats and dogs. These worms have been detected in almost all the northern seas and in the Caspian Sea (Delamure, 1955).

Field characteristics. These are rather small, predominantly coastal porpoises. The upper part of the trunk is black and the underside light-colored. The tip of the dorsal fin is almost rectangular. These animals live in small groups. Intense flexure of the body while diving is characteristic. They generally do not breach the water.

Economic Importance

Common porpoises are of almost no economic importance. Danish fishermen catch several hundreds of porpoises a year in the Little Baelt Strait during their migration from the Baltic Sea. They chase them into the narrow strait and block them in nets. In other parts of the range, the catch is only incidental.

Regular hunting of common porpoises is carried out only in the Azov and Black seas but here, too, this species is not of great economic importance. In the best years of hunting, the proportions of the different species of dolphins in the catch from this water body are: common

dolphin 200, common porpoise (from Azov Sea) 10, and bottlenose dolphin 1 (Tsalkin, 1937). This is based on a catch of 700-800 Azov Sea common porpoise; in some years up to 4,000 animals are caught and the proportions vary considerably (Bodrov, Grigor'ev, and Tver'yanovich, 1958).

548 The technique of catching the Azov Sea common porpoise, although not different from that used for catching the common dolphin, has certain special features. The much slower Azov Sea common porpoise is usually confined to small groups, distinctly separated, and in the coastal zone. Therefore, whalers spread the fleet in a broad front, advance forward in flanks, and gradually press the animals toward the coast. The net is cast after the dolphins gather in a very dense group close to the coast.

Oil, mainly melted from blubber, represents the chief product of hunting. Further, comparatively high-quality leather goods are produced and used satisfactorily in the footwear industry. Despite many successful experiments on using the flesh of Black Sea dolphins for human consumption, it has not found wide acceptance. The material remaining after obtaining the oil (musculature, skeleton, fins, viscera, etc.) is made into a flesh-bone meal which can be used as feed for farm animals or as a fertilizer. The hollow lower jaws of dolphins contain a very small amount of so-called jaw oil, from which high-quality oil is produced for lubricating fine mechanisms. In experiments, this oil froze after 10 hr of exposure to -7 to -8°C ; the oil was then filtered at this temperature and transferred to a chamber at -25°C where it did not freeze for 24 hr (Okuneva, 1934).

The total weight of the Azov-Black Sea common porpoise varies in the range 24 to 55 kg (Okuneva, 1934), or an average of 28 kg (Dragunov and Kasinova, 1951). The weight of the various trunk sections in different seasons is shown in Tables 48 and 49.

Three very large female common porpoises from the North Pacific Ocean with a body length of 178.5 cm, 173 cm, and 168 cm weighed respectively: 75.2 kg, 70.3 kg, and 73.4 kg (Scheffer and Slipp, 1948).

In the overall balance of useful products produced by hunting marine mammals in our country, common porpoises have no economic importance whatsoever. As a result of the significant reduction in the population of dolphins in the Black and Azov seas, hunting dolphins of all species (including the Black Sea common porpoise) has been totally banned since 1965. There is also no hunting in the other areas of the range of this species (in the Atlantic and Pacific oceans). (V.A.)

Genus of Dall Porpoises

Genus *Phocoenoides* Andrews, 1911

1911. *Phocoenoides*. Andrews. Bull. Amer. Mus. Nat. Hist., 30, p. 31.

Phocoenoides truei Andrews, 1911.

Small porpoises with a body length up to 2 m.

These porpoises lack a "beak". The low dorsal fin lies slightly anterior to midbody. The flippers are relatively small.

547 **Table 48. Weight of the body sections of Azov Sea common porpoise caught in October and November (Okuneva, 1934)**

Item	Male		Female	
	Weight, kg	As % of total weight	Weight, kg	As % of total weight
Total weight	24.0 - 27.0	100	37.0-55.0	100
Head	1.8 - 2.3	7.5	2.4-3.6	6.5
Skin	1.8 - 2.3	7.3-8.8	2.0-2.5	5.4-5.9
Trunk fat	7.3 - 9.2	29.3-35.4	11.5-17.5	25.3-30.6
Fins and tail	1.0 - 1.1	2.5-4.1	1.5-1.8	3.3-3.9
Muscles (flesh)	4.8 - 6.5	19.7-24.1	10.0-15.5	24.5-27.1
Trunk bones	2.9 - 4.3	10.8-16.3	3.5- 6.5	9.5-11.8
Brain	0.3 - 0.4	1.2-1.4	—	—
Tongue	0.1 - 0.2	0.5-0.6	0.15	0.40
Blood	—	—	1.0	2.17
Viscera, inclusive of:	3.4 - 4.2	10.6-15.4	6.0-8.5	13.0 - 17.7
Liver	0.5 - 0.6	1.7-2.3	1.1-1.6	2.0-3.3
Heart	0.15	0.62	0.15	0.40
Lungs	0.6 - 0.8	2.1-2.8	1.0-1.6	1.9-3.3
Stomach and intestine	1.4 - 1.6	5.2-6.2	5.1-5.8	10.4-10.5
Kidney	0.1 - 0.2	0.3-0.6	0.20	0.36

548 **Table 49. Weight of Azov Sea common porpoise in the spring catch (2,611 animals) (Tomilin, 1957)**

	Total weight, kg	Average weight, kg	As % of total weight
Total weight	78,888	30.2	100
Blubber	32,026	12.3	40.6
Muscles (flesh)	24,018	9.2	31.2
Fins	2,956	1.1	3.7
Liver	1,566	0.6	2.0
Heart	263	0.1	0.3

The body color is dark (from dark steel to black). A large white patch occurs on each side of the body. The dorsal fin is partly or wholly white.

The broad and flattened rostrum is shorter than the cranium. The pterygoid bones are separated. The teeth are very small and number 19-23-28. Vertebrae 92-98. Phalangeal formula: I₁₋₂, II₆₋₇, III₄₋₆, IV₂₋₃, and V₁₋₂. Ribs 15-18 pairs, of which 3-5 anterior ones articulate with the sternum.

549 Biology of Dall porpoise has not been well studied. They feed on cephalopods and fish.

They are distributed in the North Pacific Ocean.

The genus comprises a single species, *P. dalli* True, 1885.

There is no hunting of this species. (V.S.)

DALL PORPOISE

Phocoenoides dalli True, 1885

1885. *Phocoena dalli*. True. Proc. U. S. Nat. Mus., 8, p. 95.

1911. *Phocoenoides truei*. Andrews. Bull. Am. Mus. N. H., 30, p. 32.

Waters of the eastern coast of Japan; Rikuzen Peninsula, Hondo Island. (V.H.)

Diagnosis

Only species of the genus.

Description

The external appearance is similar to that of other common porpoises. The body is shortened and the anterior half is somewhat thickset. The head is short (Fig. 316). The upper jaw is slightly shorter than the lower. The dorsal fin forms a near-equilateral triangle, slightly concave along the posterior margin. The length of the base of the dorsal fin is 1.7-2.2 times its height. A few small horny tubercles are present on the anterior margin of the dorsal fin. High longitudinal keels are present on the caudal stem, both in the upper and lower parts. These keels increase with age. The flippers are short and have a broad base.

The color of the head, dorsum, upper anterior and entire posterior part of the caudal stem is dark, from dark steel gray to black. A large white patch occurs on each flank and extends anteriorly up to the level of the anterior margin of the dorsal fin (*P. d. dalli*) or almost right up to the eye (*P. d. truei*). This patch posteriorly extends along the flanks of the caudal stem to the level of the anal opening but does not reach the



Plate IV.

[Dall porpoise], *Phocoenoides dalli* True, Pacific Ocean (figure by N. N. Kondakov).

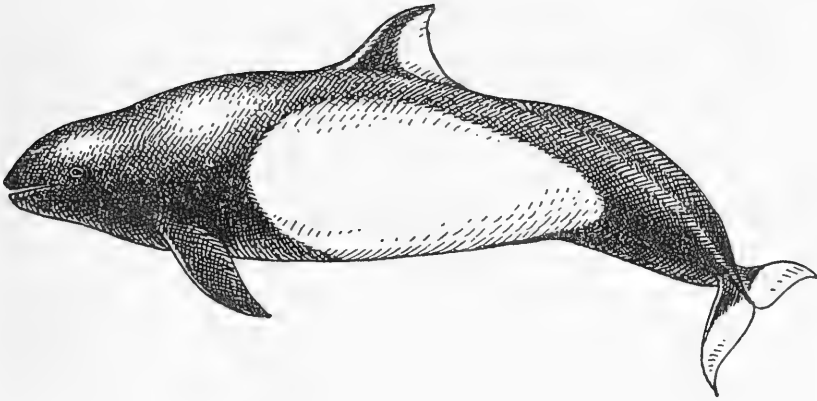


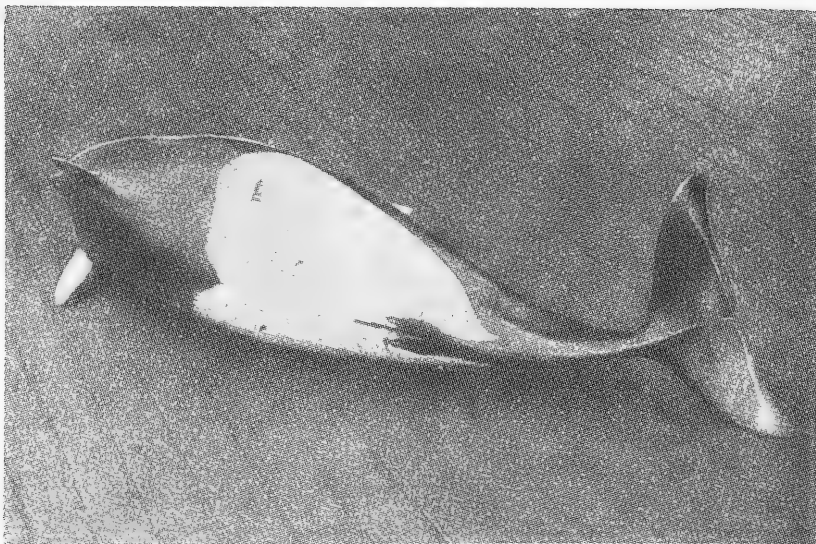
Fig. 316. Dall porpoise, *Phocoenoides dalli* (figure by N.N. Kondakov).

549

abdomen. Individuals with a coloration intermediate between these two
550 types have been sighted. The dorsal fin is wholly or partly white (dark
only rarely). The flippers are somewhat lighter in color than the trunk,
even white in exceptional cases. Totally black specimens have also been
encountered (Nishiwaki, 1966). Young animals are usually more deeply
pigmented and newborn calves less pigmented than adult animals.

The teeth are small, chisel-shaped, and barely rise above the gums.
Tubercles of keratinized epithelium are present on the gums around
the teeth. Some teeth may not cut through the gums. Thus, in an adult
male, 5 of 15 teeth in the left half of the upper jaw and 9 of 16 in
the right half had not emerged; 4 of 22 in the left half of the lower
jaw and 4 of 22 in the right half were likewise unexposed (Benson and
Grood, 1942). The interalveolar septa are poorly developed. The teeth
are surrounded by tubercles of keratinized epithelium of the gums which
could rise above the tooth crowns and function as a substitute or them.
Cervical vertebrae 7, thoracic 15-18, lumbar 23-27, and caudal 39-49.
The cervical section constitutes 3%, thoracic 23%, lumbar 33%, and
caudal 41% of the length of the vertebral column. The vertebrae have
a flattened centrum and a long thin spinous process reaching maximum
height in the lumbar section. All the cervical vertebrae are fused.

The minimum and maximum body lengths in 14 adult male and 13
adult female Dall porpoises were respectively (in cm): 172 and 210 (\bar{x}
186) and 169 and 197 (\bar{x} 181) (Mizue and Joshida, 1965). The main body
measurements of two male Dall porpoises, one caught off the coast of
Japan and the other from the Aleutian Islands, and a female caught
off the coast of Japan (Tomilin, 1957; Norris, 1966) were respectively
(in cm): body length 191, 183, and 182; distance from tip of snout to
anterior margin of blowhole 25, 23, and 15; the same up to axilla 41, 36,



550 Fig. 317. Dall porpoise, *Phocoenoides dalli*, on the deck of a ship. Sea of Japan, 1965 (photograph by A.E. Kuzin).

551 and 24; length of flippers 23, 20, and 23; maximum width of flippers 22, 10, and 10; height of dorsal fin 16, 15, and 16; width of caudal flukes (from tip to tip) 47, 47, and 47; and distance from anal opening to fork of caudal flukes 62, 58, and 51. The largest male caught to date had a body length of 210 cm and the female 198 cm.

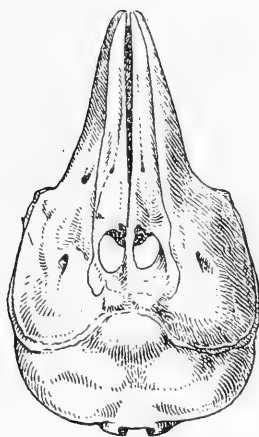
The skull measurements (Fig. 318) (average of three to five animals; Tomilin, 1957) were (in cm): condylobasal length 32, zygomatic width 19, length of rostrum 13, width of rostrum at base 10, length of lower jaw 25, and length of mandibular symphysis 3.7. (V.S.)

Geographic Distribution

This species is encountered in the North Pacific Ocean.

Geographic Range in the USSR (Fig. 319)

Coasts of the Sea of Japan commencing from Peter the Great Gulf, La Perouse Strait, waters of Sakhalin including the Gulf of Sakhalin and Kuril Islands, southeastern part of the Sea of Okhotsk, and western coast of Kamchatka. In the Bering Sea, it is encountered along the eastern coast of Kamchatka, in waters of Koryak land, Gulf of Anadyr and Bering Strait, and the adjoining waters of the Chukchi Sea.



550 Fig. 318. Skull of the Dall porpoise, *Phocaenoides dalli* (figure by N.N. Kondakov).

Geographic Range outside the USSR (Fig. 320)

Waters of the eastern and western coasts of Japan, Aleutian Islands, and eastern part of the Bering Sea, Gulf of Alaska, and along the American mainland in the south up to 30° N lat. (McTaggart, 1944; Wilke, Taniwaki, and Kuroda, 1953; Tomilin, 1957; Hall and Kelson, 1959). (V.A)

553

Geographic Variation

Two well-distinguished subspecies, also encountered in our waters, are recognized in this species. Some researchers, however, do not recognize these forms while others treat them as independent species. Details of distribution at the points of contact of the ranges, the numerical ratios between the two forms at such places, etc. are not available. Their ranges in our southern waters overlap.

1. **Northern Dall porpoise**, *P. d. dalli* True, 1885. The white patch on the flanks and ventral side of the body does not extend to the flippers but terminates roughly on the vertical of the anterior margin of the dorsal fin.

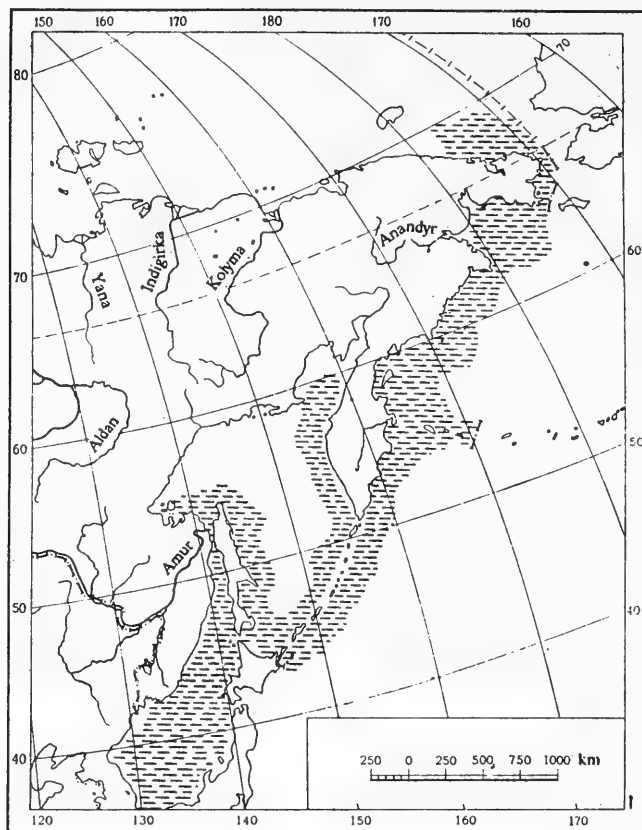
This subspecies is encountered in the waters south of Ussuri territory (Peter the Great Gulf and Pos'et Bay) and the southern islands of the Kuril range to the southern part of the Chukchi Sea inclusive.

Outside the USSR, this subspecies is reported in the waters of the Korean peninsula and Japan in the south up to roughly 38° N lat. and in American waters from the Chukchi Sea up to roughly 34° N lat.

2. **Southern Dall porpoise**, *P. d. truei* Andersen, 1911. The white patch on the flanks runs anteriorly beyond the base of the flippers and almost reaches the eye; on the abdomen, it runs from the base of the caudal stem to the base of the flippers. A small white patch occurs on the throat.

This subspecies is reported in the waters of the southernmost parts of Ussuri territory (Primor'e) in the north up to 42 to 43° N lat. (Pos'et Bay, Peter the Great Gulf, and more eastward), and possibly in the southern part of the Kuril range.

Outside the USSR, it is reported in the waters of the Korean peninsula and Japan between 38° and 43° N lat. Along the American coast, it



551 Fig. 319. Range of the Dall porpoise, *Phocoenoides dalli*, in the USSR (V.A. Arsen'ev).

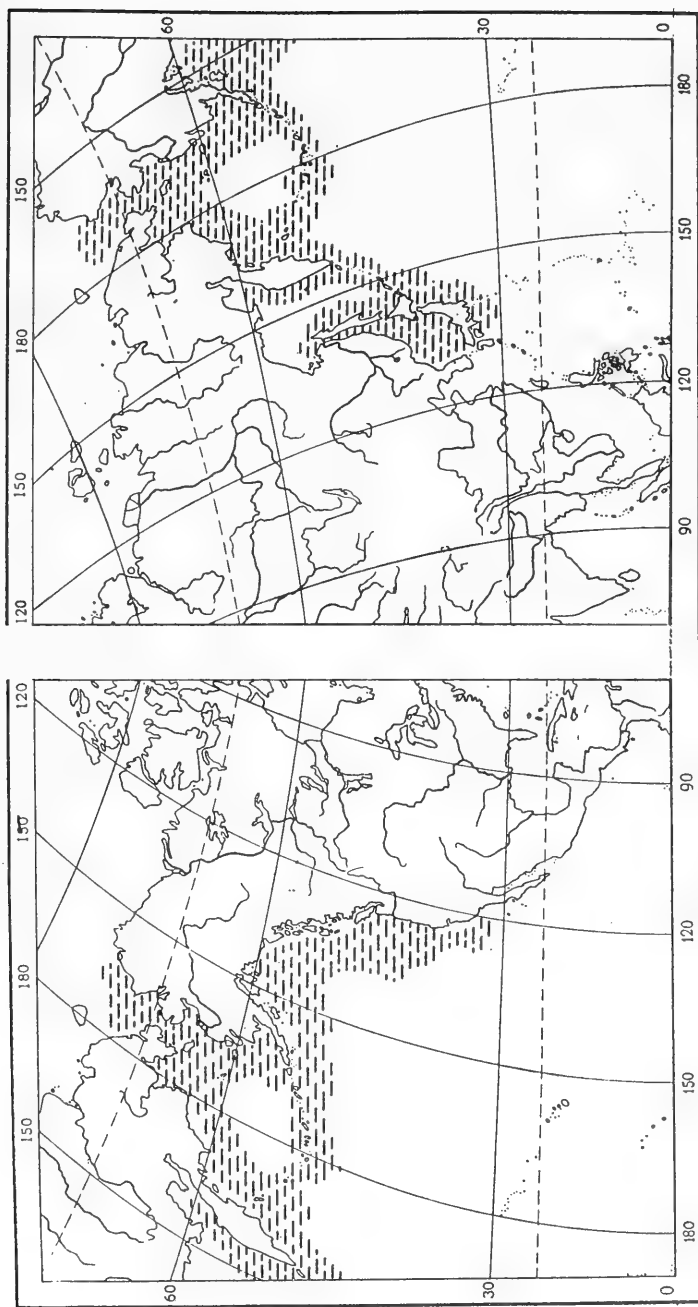


Fig. 320. Species range of the Dall porpoise, *Phocoenoides dalli* (V.A. Arsen'ev).

has been indicated from 28-30° N lat. to 45-50° N lat. (Klumov, 1959; Nishiwaki, 1966).¹⁶ (V.A.)

Biology

Population. Probably, one of the relatively abundant species, forming at times large herds of hundreds of animals. It is apparently quite abundant in the western parts of the Pacific Ocean along the coasts of Japan and the Kuril Islands.

Food. Pelagic schooling fish and cephalopods constitute the main food. Food composition varies in different parts of the range. The stomach of six animals of the northern subspecies caught in the waters of California and Oregon states contained hake (pike) (*Merluccius productus*), jack mackerel (*Trachurus symmetricus*), and squids (*Loligo opalescens*); the stomach of four animals from British Columbia contained herring, while capelin (*Mallotus villosus*) was found in the stomach of two animals from the Gulf of Alaska. Lantern fish (few species) are of overriding importance in the waters of Japan and squids and other species of fish are of lesser importance (Wilke and Nicholson, 1958). In the Bering Sea, along the islands of the western part of the Aleutian range and on the coasts of Kamchatka, squids predominate in the food (Fig. 321) while smaller fish and shrimps are consumed to a lesser extent. In most of the cases examined, various species of animals were found together in the stomach of porpoises (Mizue, Joshida, and Takemura, 1966). The species of cephalopods and fish found in the stomachs have not been stated.

The food composition of northern and southern Dall porpoises compiled from specimens collected in the waters of Japan from March through June is compared in Table 50.

554 Fishes of the family Sudidae are considered very rare and only rare specimens are found in ichthyological collections; nevertheless common porpoises apparently feed on them quite regularly. The stomach of the porpoises caught in the Sea of Japan contained saury and squids (Sleptsov, 1955).

Behavior. Dall porpoises are most often encountered in small groups of 2 to 18 head but herds of 20 to 25 animals have been encountered

¹⁶ Hall and Kelson (1959) do not recognize this form and regard Long Beach and Los Angeles at 34° N lat. as the southern point of this range.

According to the data of A.G. Tomilin (1957), our northern form covers the Sea of Okhotsk and Bering Sea as also the Sea of Japan. His more recent references correspond to those cited in the text. (V.H.)



Fig. 321. Squids in the stomach of a Dall porpoise. Pacific Ocean, east of Honshu Island, 1960. (photograph by G.M. Kosygin).

in the fore-Kuril waters (Fig. 322). Sometimes herds of these dolphins contain 100 or more animals.

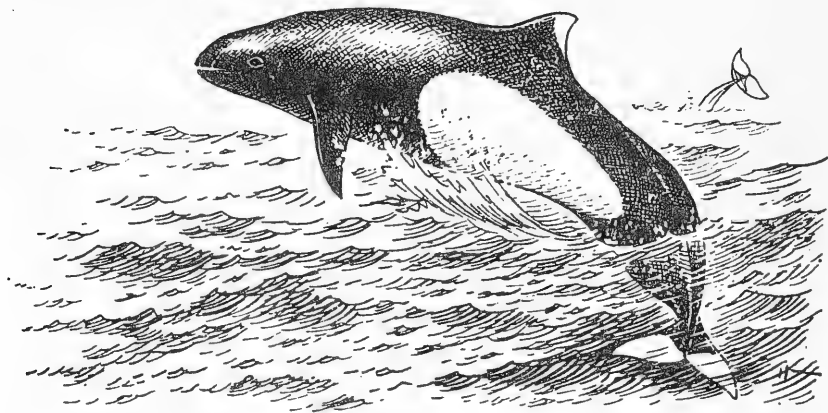
While in motion, these porpoises breach the water often and sharply so, flying in the air over quite a long distance. On finding themselves in the vicinity of a ship, they run rapidly ahead of its bow, quickly changing from side to side, or swim along the board, easily overtaking the ship. The speed of these porpoises exceeds 20 km/hr.

These porpoises are sighted close to the coasts as also far away from them in deepwater regions. The dolphins studied off the coasts of North America were caught at depths of 180 m and off the coasts of Japan at depths of 2,700 m.

555 *Migrations.* Information on migrations is extremely fragmentary. In the northern parts of their geographic range, especially at the places of ice cover, these dolphins move from south to north and back, spending the winter season outside the ice-covered regions. Apparently, comparatively small seasonal migrations are a feature of these porpoises in the other parts of their range also.

Table 50. Food of Dall porpoises (Wilke and Nicholson, 1958)

Food item	Southern subspecies (86 animals)		Northern subspecies (7 animals)	
	Number of stomachs	% by vol.	Number of stomachs	% by vol.
Fishes				
Lantern fishes:				
<i>Notoscopelus</i> sp.	27	21	2	37
<i>Diaphus</i> sp.	6	2	—	—
<i>Tailetonbeania taylori</i>	5	1	3	11
<i>Lampanyctus</i> sp.	1	Traces	—	—
Unestablished species	44	49	3	35
Suidae— <i>Paralepis</i> sp.	7	4	2	10
Hake, <i>Laemonema longipes</i>	5	11	—	—
Mackerel, <i>Scomber japonicus</i>	2	1	—	—
Squids				
<i>Ommatostrephes sloanei-pacificus</i>	22	5	1	2
<i>Watasenia scintillans</i>	35	6	3	3
Unestablished species	5	Traces	2	Traces

Fig. 322. Dall porpoise, *Phocoenoides dalli*, at sea (figure by N.N. Kondakov).

In the Pacific Ocean waters along the Canadian coast, Dall porpoises were encountered in summer mainly in the bays between the islands north of Vancouver Island. The animals prefer bays which are wide open on both sides with characteristic ebb-tide currents.

In the waters of Japan, early in March, Dall porpoises are caught in the southern part of the range; large herds of these animals are seen in mid-March in the waters of Iwata Prefecture (about 40° N lat.). Hunting here continues up to June. Later, most of the porpoises migrate to the

coasts of Hokkaido and are caught again in autumn along the coasts of Honshu.

In the coastal waters of the islands of Japan, hunting is carried out within the 30-mile coastal limit but most of the animals are concentrated in the summer at a distance of 10 to 15 miles from the coasts (Wilke, Taniwaki, and Kuroda, 1953).

Reproduction. In May, 1950, embryos weighing over 6 kg were found in the females of the northern subspecies (Wilke *et al.*, 1953). A fully formed embryo was found in a female porpoise in the waters of Queen Charlotte Island in November, 1926. It is possible that the period of parturition is greatly extended among these porpoises. South of Queen Charlotte Island, newborn calves were often sighted in August and not even once encountered before August 7.

A large number of animals was studied over several years in the southwestern part of the Bering Sea from the second half of May to early August. Fully mature testes were not seen in the male porpoises during this period. Evidently, their mating occurs later, probably not earlier than August end. This is also supported by the results of studying the female reproductive systems: corpora lutea were not detected in the ovaries of females.

The period of parturition has tentatively been placed in the second half of July to mid-August. Gestation among animals of this species thus extends for not less than a year. Among all the pregnant females, without exception, embryos lay exclusively in the left horn of the uterus; the state of the left horn indicated that the embryo had formed in it and the corpus luteum was present in the left ovary. Graafian follicles in the ovaries of all the nonproducing females, without exception, had developed in the left ovary while the right one appeared to be immature. Among the embryos, no difference was detected between the left and right ovaries but in a newborn calf the left ovary was already larger than the right one.

Based on a small number of samples, it was tentatively determined that the body length of a calf at birth is 85 - 90 cm. Most females become mature after two full years and a body length of about 170 cm. Males achieve sexual maturity at the age of three years or even older and a body length roughly of 185 cm. The ratio between the males and females in the population is close to 1:1. Of the 54 animals studied, 26 were females and 28 males (Mizue and Joshida, 1965; Mizue, Joshida, and Takemura, 1966).

A slightly different distribution of animals of different sexes has been noticed among the southern subspecies. As established from the results

of spring hunting (from March through May), males remain in the southern and females in the northern half of their range (Wilke *et al.*, 1953).

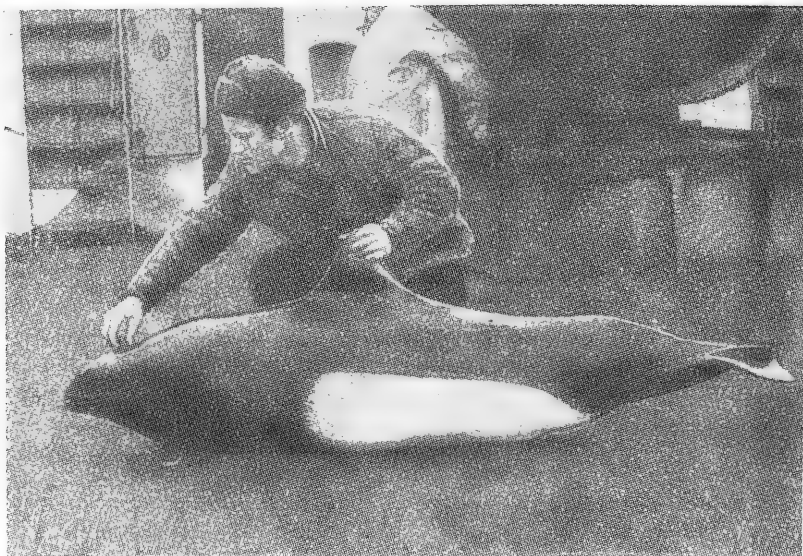
Enemies, diseases, parasites, mortality, and competitors. The nematode *Halocerus (Prohalocerus) kirbyi* Dougherty, not known among other marine mammals, has been detected in the lungs of animals from San Franciscan waters. *H. dalli* and *Irukanema dalli* are also known. In the stomach of a lone dissected animal from waters of the Kuril Islands, an immature *Anisakis* sp. was detected (Delamure, 1955; A. Skrjabin, 1960).

Field diagnosis: Sharply demarcated large white patches ("wings") on the sides and a white smear on the dorsal fin are characteristic of this dolphin (Fig. 323). (V.A.)

Economic Importance

This species is of limited hunting importance only in Japan where up to a thousand or even more porpoises are caught each year. No catches have been reported from other parts of the range.

Dall porpoises are hunted along with other species of dolphins and small whales, using small craft (20-30 tons) with a crew of 10-12 persons. These vessels are used in spring to catch these porpoises and sharks
557 and swordfish in summer; these vessels are again used in spring to catch



porpoises. These ships cruise at 7-10 miles/hr. Shooting with guns and harpooning the killed animals manually is done from a special wooden platform constructed on the bow. From time to time, when the porpoises approach the vessel quite close, they can be harpooned without using firearms. In most cases, the killed porpoise floats on the water surface for a few minutes in a vertical position with the head above the water. Killed porpoises have even been found floating a day or two days after shooting. Nevertheless, a large number of killed animals escape the hunter's bag. Thus, in 1950, about one-third of the killed Dall porpoises were lost.

With the growing salmon fisheries in the open sea, Japanese fishermen have begun catching a large number of Dall porpoises every year. The regions of porpoise catching have been identified as regions in which the salmon are caught using gill nets. This catch is practiced in the north-western part of the Pacific Ocean and in the southwestern part of the Bering Sea, including coastal waters of the Aleutian island range and Kamchatka coasts. Porpoises fall into salmon nets in coastal waters more often than in the open sea. It has been assumed that porpoises are also abundant east of this region of salmon catching, where salmon are not fished. Porpoises probably become entangled in the nets when they feed on the fish caught in them. However, an analysis of their stomach contents did not reveal a significant number of salmon. In some years, some tens and even more than a thousand Dall porpoises fall into salmon nets, but until recently these porpoises were not utilized and fishermen threw them overboard (Mizue and Joshida, 1965).

The output of Japanese porpoise hunting is disposed mainly in the market. The carcass is prepared for sale as follows. The flippers dorsal fin and caudal flukes are dismembered. Two longitudinal sections are made through the skin (along the dorsum and belly) from the tip of the snout to the tail. Later, blubber with the skin is separated from the trunk in two pieces. The flesh is separated from the vertebral column, also in two pieces, the ribs cut out, and the abdominal cavity cleared by removing the intestine, heart, liver, and kidneys, which are sold as edible products. The skin is tanned but the product is of rather poor quality. Oil is rendered from the blubber; fat from the head and jaw regions serves as raw material for producing excellent machine oil. Skeletal bones and all other remnants are processed into a fertilizer meal. The flesh is quite often used as food.

Females weigh 91 - 115 kg (M 95 kg) and males 84 - 118 kg (M 102 kg) (McTaggart, 1944; Wilke, Taniwaki, and Kuroda, 1953; Klumov, 1959). (V.A.)

Genus of Black Finless Porpoises

Genus *Neophocaena* Palmer, 1899

1846. *Neomeris*. Gray. Zoology. Voyage Erebus and Terror, I, Mamm., p. 30. *Delphinus phocaenoides* G. Cuvier. Nom. praeocc. (*Neomeris* Costa, 1844, from the group *Vermes*).

1847. *Meomeris*. Gray. List Osteol. Spec. Brit. Mus., pp. XII, 36. Not important from nomenclatural viewpoint.

1899. *Neophocaena*. Palmer. Proc. Biol. Soc. Washington, 13, p. 23. Substituted for preoccupied *Neomeris* Gray, 1846. (V.H.)

Maximum body length, up to 190 cm.

The head is rounded. No "beak" is evident. A dorsal fin is lacking. A band of fine horny tubercles runs along the middorsal line.

The body is lead-black but the abdomen light-colored.

558 The rostrum of the skull is rounded anteriorly, broad, and short (much shorter than the cranium). The premaxillae are broad and not pinched anteriorly. The small pterygoid bones are widely separated. The teeth have broadened and flattened crowns and number $\frac{15-19}{15-19}$. Vertebrae 60-63. Phalangeal formula: I_2 , II_{5-7} , III_{5-6} , IV_3 , and V_2 . Ribs, usually in 14 pairs.

Almost nothing is known about the biology of these animals. They feed on bottom-dwelling crustaceans, fish, and cephalopods.

They inhabit the warm waters of the Indian Ocean and the western part of the Pacific Ocean. They usually live near the coasts and transgress into rivers. They have been reported from the Far Eastern waters of the USSR but none have been caught.

The genus comprises a single species, *N. phocaenoides* G. Cuvier, 1829. (V.S.)

BLACK FINLESS PORPOISE

Neophocaena phocaenoides G. Cuvier, 1829

1829. *Delphinus phocaenoides*. G. Cuvier. Règne animale, I, p. 291. Cape of Good Hope, South Africa. (V.H.)

Diagnosis

Only species of the genus.

Description

Similar to the other common porpoises in outer appearance. The body build is compact. The trunk is somewhat stunted and thickened in the anterior portion. The head is relatively short (Fig. 324). The adipose

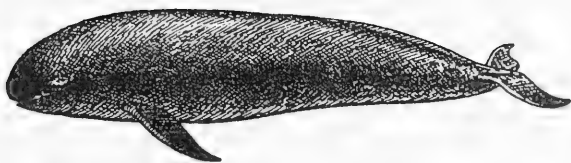


Fig. 324. Black finless porpoise, *Neophocaena phocaenoides* (figure by N.N. Kondakov).

body (corpus adiposum) [melon] on the head is highly developed and projects forward in the frontal part. The mouth section is small and its corners are upturned. The flippers are quite broad and crescent-shaped. Along the middorsum, from the cervical section to the anus, a band of horny tubercles, 3-6 cm wide, occurs, which broadens slightly anteriorly and narrows posteriorly. Much larger tubercles (up to 0.5 mm high and 2-2.5 mm in diameter) occur along the margins of the band. In the embryos, these tubercles are disposed one each on quadrangular plates closely adjoining each other. The upper lip of the embryo sports eight whiskers (four on each side).

The lead-black color on the upper side of the body gradually lightens notably on the abdomen. A gray patch is visible on the thorax and abdomen. The flippers and caudal flukes sometimes have light-colored sections of varying size. Cervical vertebrae 7, thoracic 13-14, lumbar 11-14, and caudal 28-31. The first five cervical vertebrae are fused.

The main body measurements of an adult female black finless porpoise (Tomilin, 1957) are (in cm): body length 124; distance from tip of snout to anal opening 8.5, to base of flippers 23, to posterior margin of blowhole 9; width of caudal flukes from corner to corner 43; maximum length of flippers 26 and maximum width 8.

The measurements of the skull (Fig. 325) of a male black finless porpoise with a body length of 116 cm are (Tomilin, 1957) (in cm): condylobasal length 19, zygomatic width 12, length of rostrum 7, width of rostrum at base 6, length of lower jaw 13, and length of mandibular symphysis 1.5.

In the skeleton of one male (length of vertebral column 85 cm) there were 7 cervical vertebrae, 12 thoracic, 14 lumbar, and 25 caudal; the cervical section constituted 4.5%, thoracic 27.6%, lumbar 37.2%, and caudal 30.7% of the vertebral length (Tomilin, 1957) (it is possible that some caudal vertebrae were lost). (V.S.)

Geographic Distribution

Warm waters of the western part of the Pacific Ocean and the Indian Ocean.

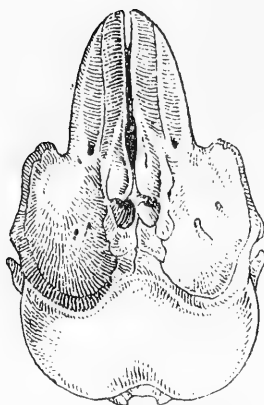


Fig. 325. Skull of the black finless porpoise, *Neophocaena phocaenoides* (figure by N.N. Kondakov).

Geographic Range in the USSR (Fig. 326)

Pacific Ocean waters of the southern Kuril Islands; transgressions are possible into the waters of the Sea of Japan.¹⁷

Geographic Range outside the USSR (Fig. 327)

Waters of Japan, Korean peninsula, China (South China Sea), Kalimantan and other islands, and also Malaccan peninsula. It is known in the Indian Ocean in the Bay of Bengal and the Persian Gulf, the Arabian Sea, and along the coasts of Africa up to the Cape of Good Hope (Sleptsov, 1961; Tomilin, 1962). (V.A.)

Geographic Variation

Not established.

Biology

Information on biology is extremely scant. Crustaceans (macrura group: *Penaeus*, *Palaemon*, and especially *P. japonicus*), cephalopods (*Loligo* sp. and *Sepia* sp.), and some species of fish serve as food objects. They consume predominantly benthic animals and hence the black finless porpoise can be regarded as a coastal form. According to observations made

¹⁷ Once, in 1951, two porpoises were encountered 20 to 25 miles off Shpanberg Island in the southern Kuril Island range (Sleptsov, 1952). This species has not been caught in our waters.

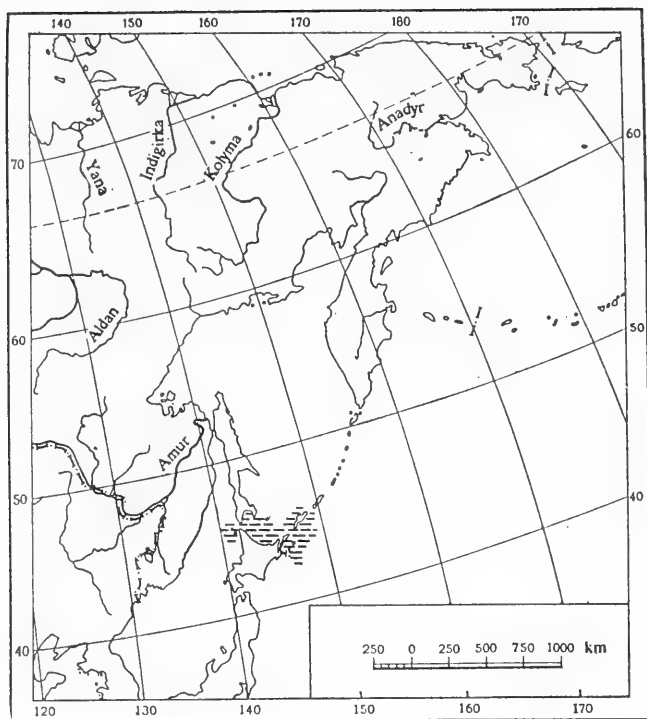


Fig. 326. Range of the black finless porpoise, *Neophocaena phocaenoides*, in the USSR (V.A. Arsen'ev).

on the Kuril Islands (Sleptsov, 1961), it is encountered in open waters, mainly in small groups (five or six animals) and singly. Sometimes the animals gather far away from the coasts into very large herds consisting of several tens of animals. Quite often, they transgress into rivers in which they spend much time, ascending hundreds of kilometers upstream (along the Yangtze up to 1,800 km; also sighted in Lake Dongting Hu). Their movements are gentle and they rarely breach the water.

Migrations have not been studied. It has been assumed that parturition occurs in October since a female 119 cm long with an embryo 52 cm long was encountered in this month.

561 Seven species of helminths have been registered among black finless porpoises: trematodes three, cestodes one, and nematodes three. The trematodes *Campula folium* Ozaki, *Orthosplanthus elongatus* Ozaki, and

Nasitrema spathulatum Ozaki were detected in the waters of Japan and are known only in the black finless porpoise. The first parasitizes the liver, the second the intestine, and the third the nasal cavity. The cestode, *Diphyllbothrium fuhmanni* Hsü, detected in waters of Japan and China and parasitizing the small intestine, in addition to the black finless porpoise, has been found in spotted dolphins. All the three species of nematodes were found only in the black finless porpoise from the waters of China. *Halocercus pingi* Wu localizes in the lungs, *Sternus auditivus* Hsü and Hoeppli in the auditory organs, and *Onchocerca fülleborni* Hoeppli and Hsü in the musculature. Most of the species of helminths found in the black finless porpoise have not been detected in other marine mammals.

The black finless porpoise has no economic importance whatsoever; it is not hunted except for a few stray animals caught in the rivers of China (Delamure, 1955; Sleptsov, 1955, 1961; Tomilin, 1957, 1962). (V.A.)

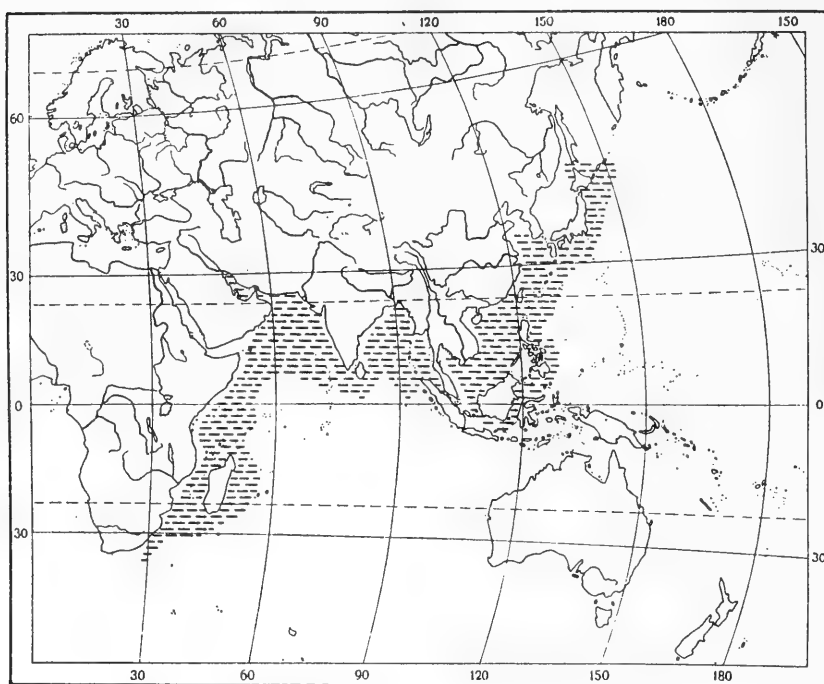


Fig. 327. Species range of the black finless porpoise, *Neophocaena phocaenoides* (V.A. Arsen'ev).

Family of Narwhals

Family MONODONTIDAE Gray, 1821

Cetaceans of medium dimensions, with body length up to 610 cm.

A dorsal fin is absent although a long low fold occurs on the dorsum. The head is rounded, small, without a beak, and demarcated from the trunk by a distinct neck. The flippers are short and broad.

Body coloration is subject to age-related variations: it is dark in young animals, turning light with advancing age.

562 The rostrum is relatively short and broad. The frontal and interparietal bones form a crest. The petrous temporal bone grows toward the skull. The broad pterygoids articulate with the squamosals. Teeth $\frac{1-11}{0-11}$. Vertebrae 49-55. The first and second cervical vertebrae are not fused while the rest may be fused in varying groups. The ulna has no olecranon process.

The geographic range of these animals is restricted to the waters of the northern polar region (Fig. 328).

The family comprises two genera: (1) belugas or white whales, *Delphinapterus* Lacépède and (2) narwhals or unicorns, *Monodon* Linnaeus. Belugas are of economic importance. (V.S.)

Genus of Belugas or White Whales

Genus *Delphinapterus* Lacépède, 1804

1804. *Delphinapterus*. Lacépède. Hist. Nat. Cétacées, p. XLI, 243. *Delphinapterus beluga* Lacépède = *Delphinus leucas* Pallas, 1766.

1815. *Beluga*. Rafinesque. Anal. Nat., p. 60. Substituted for *Delphinapterus* Lacépède, 1804. (V.H.)

Dimensions are the smallest in the subfamily, with a body length up to 6 m.

The body is markedly elongated. The relatively small head has a very prominent frontal projection. The monochromatic body is dark in the young, lightening to white (ivory) or yellow in the adult. The epidermis is remarkably well developed.

The relatively narrow skull is flattened dorsoventrally. The rostrum, broad at the base, is roughly 1.5 times longer than the cranium. The maxillae dorsally adjoin the bony nares and extend far backward, almost up to the occipital bones. The pterygoids are well developed. Powerful crests are typical. Teeth $\frac{5-11}{2-11}$, often irregular in form, and sometimes with supplementary cusps. Vertebrae 49-54. Some of the cervical vertebrae are fused. Of the 11-12 pairs of ribs, 5-7 pairs are fused to the sternum.

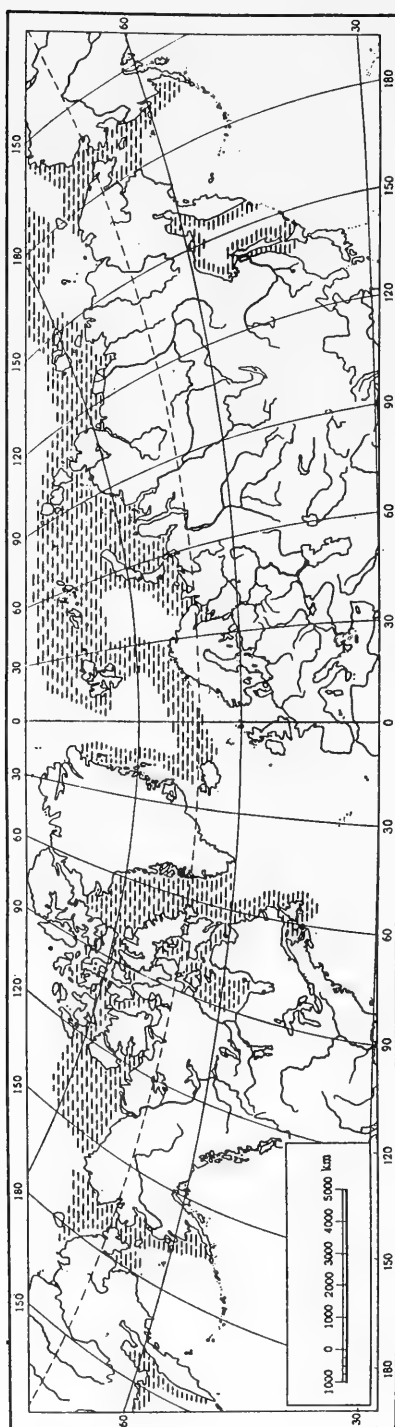


Fig. 328. Range of the narwhal family, Monodontidae (V.A. Arsen'ev).

The sternum is either non-segmented or consists of two or three sections (sometimes even six). Phalangeal formula: I_2-4 , II_6-9 , III_6-8 , IV_5-7 , and V_4-6 . Digits III and IV are almost equal in length. The number of phalanges of some digits in embryos is reduced in adult animals. Sometimes the digits are split and resemble claws.

Belugas are ichthyophagous; they feed mainly in the coastal zone of the sea. Gestation extends for 11-12 months. Females calve annually.

These animals are distributed in the seas of the North Atlantic, Arctic, and North Pacific oceans.

Fossil remains have been traced in the Pleistocene of North America. The genus comprises a single species: the beluga, *D. leucas* Pallas, 1776.

These animals are of commercial importance. (V.S.)

BELUGA OR WHITE WHALE¹⁸

Delphinapterus leucas Pallas, 1776

1776. *Delphinus leucas*. Pallas. Reise durch versch. Prov. Russ. Reiches, 3 (I), p. 497. Ob' estuary.
1776. *Delphinus albicans*. Müller, Zool. Danicae prodromus, p. 7. Greenland.
- 563 1804. *Delphinapterus beluga*. Lacépède. Hist. Nat. Cétacées, pp. XLI, 243. Davis Strait.
1935. *Delphinapterus dorofeevi*. Klumov and Barabasch. Zh. "Rybnoe Khozyaistvo SSSR," No. 11. Sakhalin Bay, Sea of Okhotsk.
1935. *Delphinapterus freimani*. Klumov. *Ibid.*, no. 7. Dvina Bay, White Sea.
1935. *Delphinapterus leucas maris-albi*. Ostroumov. Zh. Za Rybnuyu Industriyu Severa, no. 11. Onega Bay, White Sea. (V.H.)

Diagnosis

Only species of the genus.

Description

Age-related changes of body proportions are known among belugas (Arsen'ev, 1936a; Vladykov, 1943, 1944; Kleinenberg *et al.*, 1964). The changes pertain to an increase in ratio of body length to radius of the trunk and relative (to body length) reduction of length of the flippers

¹⁸ The local Russian people (coastal population) call the animal "beluga". "Belukha" represents an artificial (bookish) modification of "beluga" to distinguish the whale from "beluga fish" (giant sturgeon) (Heptner, 1930; Chapskii, 1937).

as well as narrowing of the caudal flukes. The form of the flippers of belugas is typical: their proximal margin is flexed, the flexure very distinctly manifest in old animals (Vladykov, 1943). Such a form of the flippers (Fig. 329) is possibly important for braking during sharp turns (Kleinenberg *et al.*, 1964).

The absence of a dorsal fin is explained by the adaptation of the animal to living amidst ice (the fin could interfere in floating in such conditions; Heptner, 1930) and, further, enables the animal to bend along the longitudinal axis of the body, which is important in catching fish (Yablokov, 1959). A rather low leathery crest replaces the missing dorsal fin in some animals.

The epidermis (up to 7-11 mm) and the horny layer [stratum corneum] (up to 1-6 mm) are highly thickened; the dermal layer is very well developed while the subcutaneous adipose tissue is relatively thicker compared to other whales (Bel'kovich, 1959; Kleinenberg *et al.*, 1964).

Age-related changes of body color are significant. The light gray color of the newborn changes after a few days or a week into almost black in suckling calves, but lightens gradually thereafter (Bel'kovich, 1959). Whitening is more rapid on the dorsum, body flanks, and abdomen. However, the dark-colored edge of the caudal flukes undergoes no depigmentation. The body surface of most of the animals is covered in numerous scars, spots, and stripes.

563 The white color of the belugas is considered a protective adaptation (Kükenthal, 1900). It has also been suggested that such a coloration frightens schools of fish, which facilitates their catch by the whale (Yablokov, 1956). Another view (obviously erroneous) holds that the white coloration reduces heat dissipation from the body of the animal (Chapskii, 1941). Four color groups of belugas (Fig. 330), corresponding

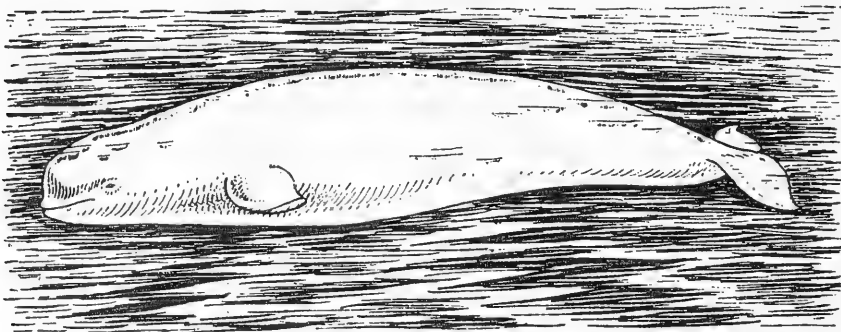


Fig. 329. Beluga, *Delphinapterus leucas* (figure by N.N. Kondakov).

to definite age groups (Dorofeev and Klumov, 1936), are usually recognized (for more details, see p. 782). However, it has been opined that the variations in coloration of the beluga body should not be taken as an accurate criterion for determining the age of these animals (Bel'kovich, 1959).

The simple peg-shaped teeth of belugas are characterized by a typical cutting and supporting form developed as a consequence of the wearing down of the teeth (Yablokov, 1958a, 1959). The maximum length of the teeth in the upper jaw is 5.8 cm and thickness 1.2 cm; in the lower jaw, 5.0 cm and 1.8 cm respectively (Yablokov, 1959). The largest teeth occur in the anterior part of the upper jaw and midpart of the lower jaw. Teeth are usually lacking on the premaxillae. Teeth are cut in year-old calves. Cervical vertebrae 7, thoracic 11-12, lumbar 6-12, and caudal 21-26.

The anterior portion of the digestive tract of the beluga, right up to the second chamber of the stomach, is covered with keratinized stratified epithelium in which (up to the first chamber of the stomach inclusive) a network of tonofibrillae, reinforcing the epithelium, is well developed. Such adaptations help the animal to swallow a large quarry whole without mastication (Kleinenberg, Yablokov and Tarasevich, 1958). The stomach consists of five chambers. The intestine, length varying from 22.5 to 37 m, is not divided distinctly into a small and large intestine due to the absence of a cecum. The duodenum is highly developed; the last third of the rectum is covered by stratified epithelium forming low longitudinal nonexpanding folds, with a powerful muscular cover supplemented by a powerful anal sphincter.

Sexual dimorphism is manifest in the dimensions of the animals; males are larger than females. Moreover, the ratio of body length to radius of its cross section is more in males than females, underscoring the excellent hydrodynamic form of the male body; the caudal flukes of males are relatively larger while the flippers, on the contrary, are

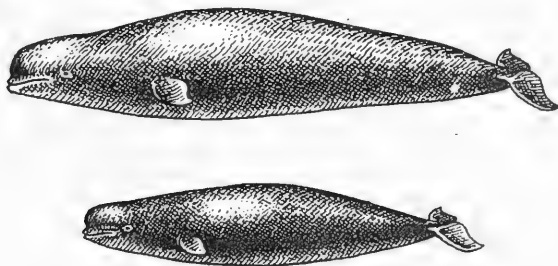


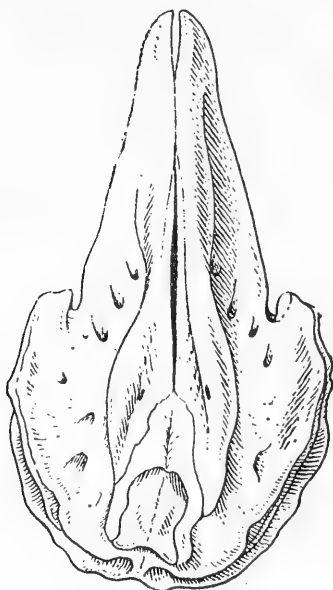
Fig. 330. Age-related color groups of the beluga, *Delphinapterus leucas* (figure by N.N. Kondakov).

relatively smaller. In males, the number of teeth is slightly more than in females (Yablokov, 1959). The frontal prominence in most males is more powerfully developed (this is particularly true of aged males).

The maximum length of belugas in the Far East is 600 cm among males and 500 cm among females; in the Kara Sea 472 and 413 cm; Gulf of St. Lawrence 447 and 409 cm; western Greenland 572 and 474 cm; Hudson Bay 448 and 400 cm; and the Beaufort Sea 460 and 383 cm (Kleinenberg *et al.*, 1964).

The main body measurements of Kara Sea belugas (Tomilin, 1957) (average for 13 - 14 males and 11 females) are respectively (in cm): body length 410 and 365; length of head 52 and 46; distance from tip of snout to base of flippers 30 and 71; distance from anal opening to fork between caudal flukes 94 and 89; length of flippers 44 and 39, width of flippers 31 and 26; and width of caudal flukes (from tip to tip) 88 and 77.

The main measurements of the skull (Fig. 331) of belugas from the White and Kara seas and the Far East (Tomilin, 1957) respectively average (in cm): condylobasal length 52 (10 measurements), 57 (10), and 59 (10); zygomatic width 28 (8), 30 (10), and 32 (4); length of rostrum 25 (10), 28 (10), and 29 (4); width of rostrum at base 17 (9), 18 (10), and 19 (4); and mandibular length 42 (4), 42 (8), and 44 (9). (V.S.)



Geographic Distribution

Predominantly the cold waters of the Northern hemisphere where it is very widely distributed almost all around the polar region.

Geographic Range in the USSR

Apparently no changes have taken place in the range over the historic past. In the Barents Sea, beluga is quite regularly encountered along the Murman coast (mainly in winter); it is sighted almost year-round at Kanin and Kolguyev, and in the Chesha Bay. It is quite common in the Pechora Sea, Vaigach, and along the west coast of Novaya Zemlya. At the end of summer, it is not infrequent around Franz Josef Land. It is most numerous probably in the southeastern corner of the Barents Sea where it is sighted throughout the year. It lives mainly along coasts and has not been sighted away from them. There is no doubt of its absence in the open Barents Sea (Fig. 332).

The beluga inhabits the entire White Sea. As an exception, it transgresses into the Baltic Sea where it has been sighted in our waters, especially in the Riga (Parnu) and Finland gulfs. In the Kara Sea, it predominantly covers the southwestern and western parts. It is encountered along the east coast of Novaya Zemlya right up to Cape Zhelaniya, at Vaigach, in Vaidarask and Gulf of Ob in Yenisey Gulf and also along the coast east up to Vil'kitskiy Strait. The beluga inhabits the Kara Sea mainly in summer. It can be encountered in autumn in its northern parts. At some places (Gulf of Ob) small herds are sometimes encountered in winter.

In the Laptev Sea, the beluga is seen in the summer months along much of the coast from Severnaya Zemlya islands to Novosibirsk. It is most common in the southwestern part of the sea (Pronchishcheva Bay, Begichev Island, etc.), and also in the Lena estuary. From the Novosibirsk islands, the beluga is seen in the waters of the East Siberian Sea. In the winter months it is probably confined to the middle and northern parts of the Laptev Sea.

It inhabits the Chukchi Sea predominantly in the summer months. Distribution along the Chukchi peninsula is restricted to the coastal section from Cape Dezhnev to Cape Shmidt but sometimes transgresses into the waters of the East Siberian Sea. Under favorable ice conditions, it moves far north. It is quite regularly found close to Wrangel Island and probably reaches 74 to 75° N lat. It is encountered in Bering Strait.

In the Bering Sea, it inhabits the Gulf of Anadyr in which it is most numerous close to the Anadyr estuary. Its distribution southward

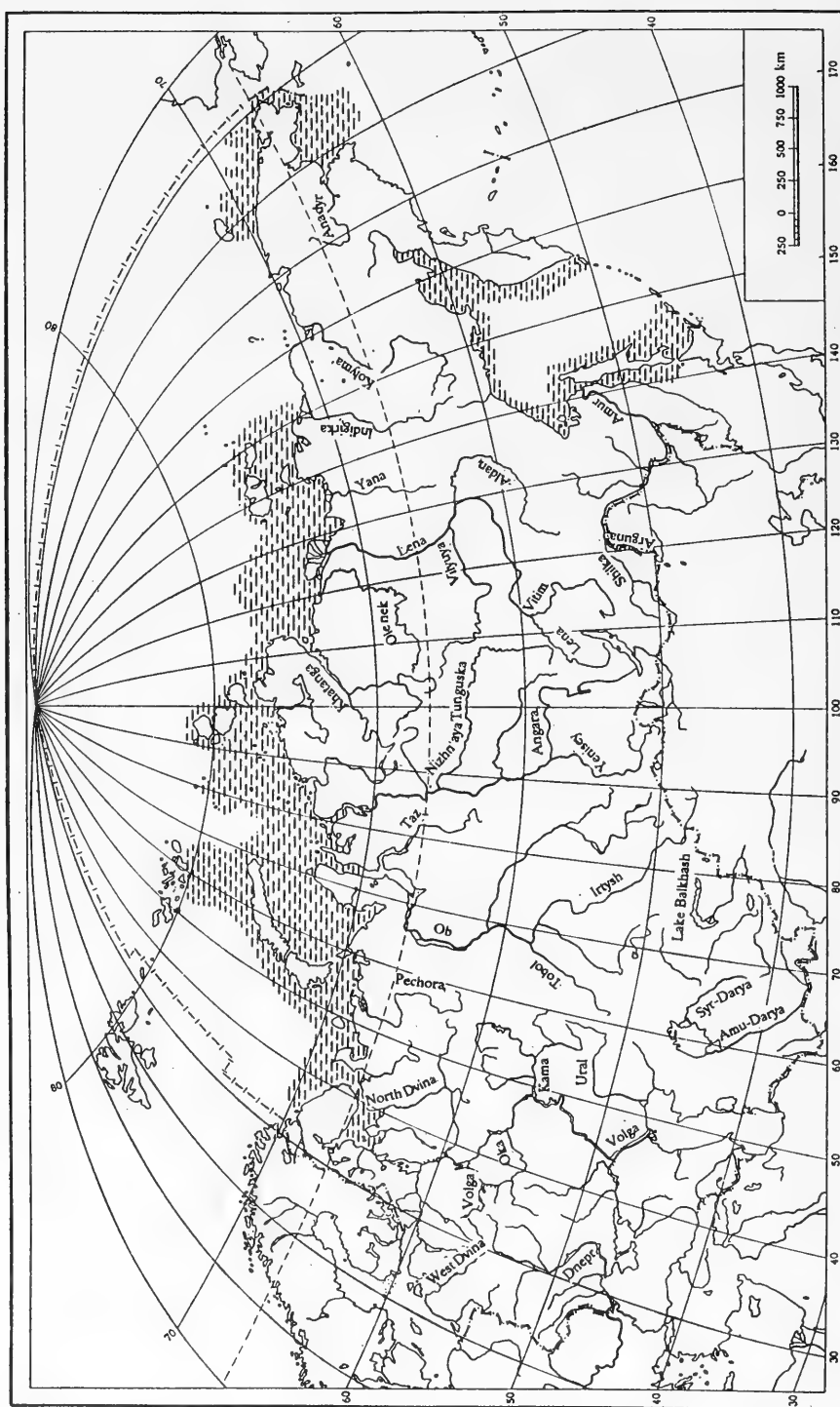


Fig. 332. Range of the beluga, *Delphinapterus leucas*, in the USSR (V.A. Arsen'ev).

is limited to Cape Navarin or only slightly farther. Distribution in the open waters of the northern part of the Bering Sea has not been studied.

567 It is found almost all along the coast of the Sea of Okhotsk. Depending on the period of the year, it is common along the Sakhalin coasts (east coast, Terpeniya Bay, La Perouse and Tatar Straits, Amur liman, and the Gulf of Sakhalin). In the southwestern part of the Sea of Okhotsk, it ranges from the Amur estuary to Uda and Ayan bays in the west. It is common along the northern coasts of the Sea of Okhotsk, including Shelikhov Gulf, and the west coast of Kamchatka, mainly its northern part. It is rare along the west coast of the Sea of Okhotsk from Ayan Bay to Okhotsk. It has not been reported in the waters of the Kuril Islands.

Geographic Range outside the USSR

In the basin of the Atlantic Ocean, it is widely distributed in the Canadian Arctic archipelago (Fig. 333). It is encountered in the Gulf of St. Lawrence, along the Labrador coasts, in Ungava Bay, Hudson Bay, Hudson Strait, Foxe Basin, Davis Strait, along the coasts of Greenland and Baffin Island, and in Baffin Bay where it reaches north of Smith Strait. It is encountered in the bays of Lancaster, Jones, and Barrow, and in the Beaufort Sea. It has been sighted in McClure Strait, Amundsen Gulf, and at many points along the coast in the region of Mackenzie Island. The beluga is also encountered east of the Canadian coast close to Iceland, Jan Mayen Island, Spitsbergen, and Finmark. Its distribution along the east coast of Greenland has not been clearly established.

In the Bering Sea, it is known along the coasts of Alaska from Bristol Bay to Bering Strait and farther, in the Chukchi Sea up to Cape Barrow on the northern coast of Alaska. It is also encountered east of this point (Arsen'ev, 1939; Vladykov, 1944; Tomilin, 1957; Sergeant, 1962a; Kleinenberg, Yablokov, Bel'kovich, and Tarasevich, 1964). (V.A.).

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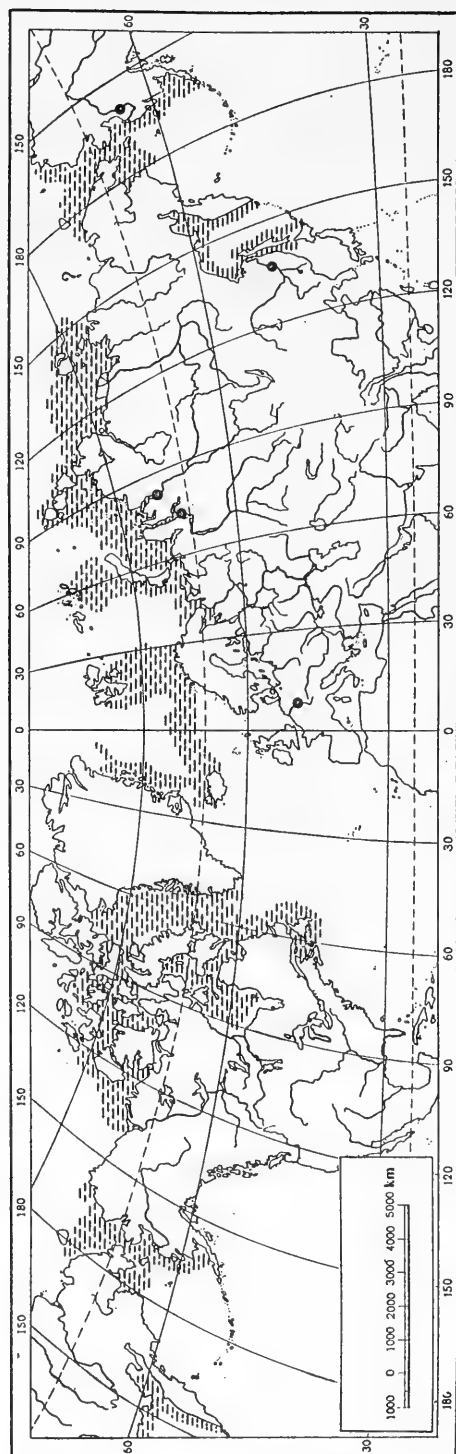
Geographic Variation

The monotypic state of the genus *Delphinapterus* has been reviewed time and again but the new species described are not usually recognized while the probability of some subspecies very recently described has invited serious dispute. Preliminarily, the existence of three subspecies of belugas may be recognized in our waters:

1. **White Sea beluga**, *D. l. maris-albi* Ostroumov, 1935. Smallest of the forms; adults 253-376 cm (\bar{x} 312).

This subspecies is found in the waters of the White Sea and the southern part of the Barents Sea.

Not reported outside the USSR.



567 Fig. 333. Species range of the beluga, *Delphinapterus leucas*. Dots represent the sites of finds of belugas in rivers (V. A. Arsen'ev).

2. **Kara Sea beluga**, *D. l. leucas* Pallas, 1776. Occupies an intermediate position among the three subspecies in body dimensions. Adults vary in length from 318 to 464 cm (\bar{x} 390).

This subspecies is found in the Barents, Kara, and Laptev seas.

Outside the USSR, it apparently lives in the remaining waters of the North Atlantic.

3. **Far Eastern beluga**, *D. l. dorofeevi* Klumov and Barabasch, 1935.

Largest of the subspecies. Adults vary in length from 320 to 600 cm (\bar{x} 424).

This subspecies is found in the Okhotsk, Bering, and Chukchi seas.

Outside the USSR, it lives in the American waters of the aforesaid seas.

A systematic analysis of belugas from the western Atlantic and eastern Pacific Oceans in relation to the above forms has not been attempted and the classification is tentative. It is possible that the populations in some of our Far Eastern water bodies are not wholly identical from the viewpoint of systematics.

Each of the subspecies occupies an immense range and it is not unlikely that many local populations exist within these ranges. Probably, belugas of the Laptev Sea form a distinct local population. Belugas from the Okhotsk and Bering seas definitely represent isolated populations, distinctly separated from each other by a large distance. Within the Okhotsk population per se, two relatively isolated herds have been postulated (see "Seasonal Migrations and Transgressions").

Belugas inhabiting waters outside the limits of the USSR also probably form several local populations. One such occupies the zone Iceland—Greenland—Spitsbergen. In Canadian waters, three such populations can be recognized: in the Gulf of St. Lawrence, in the eastern Canadian Arctic, and in the western Canadian Arctic or the Beaufort Sea. The first of these, even if it mixes at all with the eastern Arctic population, does so very minimally. The two arctic populations of America are separated by 20° along the longitude in the zone of Melville Strait (Sergeant, 1962a). However, there is as yet no adequate information to resolve this problem. (V.A.)

Biology

Population. The beluga may be regarded as a moderately populous species. According to approximate calculations, the population of White Sea beluga comprises 8,000-10,000 and of the Kara Sea 40,000-50,000 animals (Klumov, 1939). No less than several tens of thousands of animals live in the Sea of Okhotsk but the Bering Sea population is

probably somewhat less. Information is not available for judging the beluga population in other parts of the range within USSR waters. The commercial utilization of all these populations is so insignificant that hunting has no bearing whatsoever on the natural population dynamics.

Food. Fish and crustaceans serve as food objects. The extensive range occupied by the beluga provides quite a large number of species of food objects which differ in various parts of the range. However, fish everywhere occupy a predominant position. The large number of organisms found in the stomachs contain some which enter incidentally or represent the food of animals on which the beluga feeds (Table 51).

Fish (pelagic and benthic) which form massive schools and bottom-dwelling crustaceans constitute the main food. The least number of empty stomachs among the belugas of the Sea of Okhotsk is seen during the massive arrival of salmon (Arsen'ev, 1939); in the northern seas, the beluga feeds most intensely in the period of arrival of arctic cod (Klumov, 1936a; Tarasevich, 1960a, 1960b).

Based on the frequency of encounter and the number of animals found in the stomach of belugas, their main food items are: in the White Sea—herring, capelin, and shrimps; in the Kara Sea—arctic cod, cisco, and other whitefish; in the Sea of Okhotsk—salmon (chum salmon and humpback salmon), navaga, herring, and isopods; in the Gulf of St. Lawrence—capelin, sand eel, cephalopods, and *Nereis*; and in Hudson Bay—capelin, cephalopods, and *Nereis*. Arctic char (*Salvelinus alpinus*; Daan and Douglas, 1953) was additionally encountered in the stomach of belugas of the Canadian Arctic.

A seasonal change of food intake, also having a bearing on the age of belugas, has been noticed. For the White Sea beluga inhabiting the waters of Kanin, the main food objects in June are lumpsucker and flounder, changing to navaga, cod, and shrimps in mid-July, and herring and flounder at July end (Klumov, 1936a). In the Gulf of Sakhalin of the Sea of Okhotsk, young belugas at the end of the milk suckling period consume mainly crustaceans, which constitute up to 50% of their ration, and relatively small fish. As the animal grows, the importance of crustaceans and small fish gives place to large fish (salmon) whose specific proportion in the intake increases. Large fish serve as the main food of adult animals in which crustaceans account for less than 9% of the intake (Arsen'ev, 1939). Belugas of the Gulf of St. Lawrence also exhibit differences in food intake relative to the regions, seasons, age, and even sex groups (Vladykov, 1947).

The food of the beluga has been studied everywhere only in the summer months. No information is available on its winter sustenance.

Table 51. Food objects of belugas

White Sea (Klumov, 1936a)	Barents and Kara seas (Klumov, 1936a)
Fish	Fish
Atlantic herring, <i>Clupea harengus</i> L.	Arctic cod, <i>Boreogadus saida</i> (Lepech.)
West Atlantic capelin, <i>Mallotus villosus</i> Müll.	Arctic cisco, <i>Coregonus autumnalis</i> (Pall.)
European smelt, <i>Osmerus eperlanus dentex</i> Steind	Siberian cisco, <i>Coregonus sardinella</i> Val.
Arctic lamprey, <i>Lampetra japonica tentrionalis</i> Berg	Muksun, <i>Coregonus muksun</i> (Pall.)
Atlantic navaga, <i>Eleginus navaga</i> (Pall.)	Siberian sturgeon, <i>Acipenser baeri</i> Brandt
Lumpsucker, <i>Cyclopterus lumpus</i> (L.)	Nelma, <i>Stenodus leucichthys nelma</i> Pall.
Atlantic cod, <i>Gadus morrhua</i> L.	Pike, <i>Esox lucius</i> (L.)
Haddock, <i>Melanogrammus aeglefinus</i> (Hodd.)	Siberian powan, <i>Coregonus lavaretus pidschian</i> (Gmel.)
Flounders: <i>Pleuronectes flesus</i> P.	Atlantic herring, <i>Clupea harengus</i> L.
<i>P. platessa</i> L.	Smelt, <i>Osmerus</i> sp.
<i>Liopsetta gracilis</i> (Pal.)	Arctic char, <i>Salvelinus alpinus</i>
Crustaceans	Crustaceans
Shrimp, <i>Crangon crangon</i> L.	Isopod, <i>Mesidothea entomon</i>
	<i>Mesidothea sabini</i>
	Gammaridae
Sea of Okhotsk (V.A. Arsen'ev, 1939)	Gulf of St. Lawrence (Vladykov, 1947)
Fish	Fish
Chum, <i>Oncorhynchus keta</i> Walb.	Haddock, <i>Melanogrammus aeglefinus</i> (L.)
Humpback salmon, <i>Oncorhynchus gorbuscha</i> Walb.	Ocean pout, <i>Zoarces anguillaris</i> (Peck)
Navaga, <i>Eleginus navaga gracilis</i> Til.	Blenny, Blenniidae
Pacific herring, <i>Clupea harengus pallasi</i> Val.	Snailfish, <i>Neoliparis atlanticus</i> (Müll.)
Flounder, Pleuronectidae	Capelin, <i>Mallotus villosus</i> Müll.
Rudd, <i>Leuciscus brandti</i> Dyb.	Sculpin, <i>Myoxocephalus scorpius groenlandicus</i> (Cuvier and Valenciennes)
Smelt, <i>Hypomesus</i> sp.	Staghorn sculpin, <i>Gymnocanthus tricuspis</i> (Reinhardt)
Goby, <i>Myoxocephalus</i> sp.	American smelt, <i>Osmerus mordax</i> (Mitchill)
Pacific eelpout, <i>Zoarces elongatus</i> Kner.	Sturgeon, <i>Acipenser oxyrinchus</i> Mitch.
Blenny, Blenniidae	Atlantic herring, <i>Clupea harengus</i> L.
Arctic lamprey, <i>Lampetra japonica</i> (Martens)	Sea lamprey, <i>Petromyzon marinus</i> L.
Sakhalin char, <i>Salvelinus leucomaenis</i> Pall.	American sand lance, <i>Ammodytes americanus</i> De Kay
Okhotsk whitefish, <i>Coregonus ussuriensis</i> Berg	Atlantic tomcod, <i>Microgadus tomcod</i> (Walbaum)

Contd.

Table 51 Continued

Sea of Okhotsk (V.A. Arsen'ev, 1939)	Gulf of St. Lawrence (Vladykov, 1947)
Crustaceans	Red hake, <i>Urophycis chuss</i> (Walbaum)
Shrimp, <i>Crangon septemspinosa</i> Say	Baltic cod, <i>Gadus callaris</i> L.
Isopod, <i>Mesidothea entomon orientalis</i> Gurjanova	Greenland cod, <i>Gadus ogac</i> Reinhardt
Shrenck's crayfish, <i>Cambaroides schrenckii</i> Kessler	Witch flounder, <i>Glyptocephalus cynoglossus</i> (L.)
570 Hermit crab, <i>Pagurus capilatus</i>	Smooth flounder, <i>Liopsetta putnami</i> (Gill)
Mud shrimp, <i>Upogebia issaeffi</i> Balss.	Winter flounder, <i>Pseudopleuronectes americanus</i> (Walbaum)
Cumacea	Atlantic lumpfish, <i>Cyclopterus lumpus</i> L.
Macruran crabs	Thorny skate, <i>Raja radiata</i> Donovan
	Smooth skate, <i>Raja senta</i> Garman
	Skate, <i>Raja</i> sp.
	Atlantic salmon, <i>Salmo salar</i> L.
Mollusks	Crustaceans
<i>Mytilus edulis</i> Linné	Shrimp, <i>Pandalus montagui</i>
	Scud, amphipods
Lamellibranchiata	<i>Argis</i>
Rhizopoda	Copepods
Nemertini	Cumacea
	Schizopodes
	Cephalopods
	<i>Bathypolypus obesus</i> (Verrilli)
	Atlantic shortfin squid, <i>Illex illecebrosus</i> (Le Sueur)
	Gastropods
	Whelk, <i>Buccinum undatum</i> Linné
	Periwinkle, <i>Littorina</i> sp. (?)
	Bivalves
	<i>Crenella</i> sp. (?)
	<i>Cystodaria silgua</i> Spengler
	<i>Macoma baltica</i> Linné
	<i>Mesodesma arcata</i> Conrad
	<i>Mesodesma deaurata</i> Turton
	<i>Mesodesma</i> sp. (?)
	<i>Mya</i> sp. (?)
	<i>Yoldia limanula</i> Say
	Polychaeta
	<i>Cistendes gouldii</i> Verrill
	<i>Nereis virens</i> Sars

Daily activity and behavior. The beluga is a typical herding animal, found usually in groups of various strengths. Among numerous observations, lone animals were encountered in 16.1% of cases (Bel'kovich, 1960). A herd of belugas irrespective of its strength, invariably consists of small groups (Fig. 334) of two to four or five to eight animals (Golenchenko, 1949a). The age and sex composition of the herd can vary while the males within a herd often form independent groups. In other cases, mixed groups are formed in which young ones can also be seen along with mature animals. However, immature animals never form independent groups. In the period of reproduction, groups are noticed within a herd. These groups consist of three or more belugas, among which is a female with a suckling calf and one or two adult animals. The female in such groups probably had given birth only recently and was preparing for fertilization afresh. At the end of the reproduction period, adult males quite often segregate themselves from females and form independent herds.

The herd size varies markedly. The most frequently noticed herds comprise tens (54.9% cases) or several tens of animals (25.8%). Herds running into a few hundred animals are rare (3.2%) but herds running into a few thousands of animals can be seen in the period of massive concentrations of fish (salmon in the Far East). Small herds are invariably formed of animals chasing huge schools of fish. An analysis of hunting data shows that the male to female ratio in a herd is invariably close to

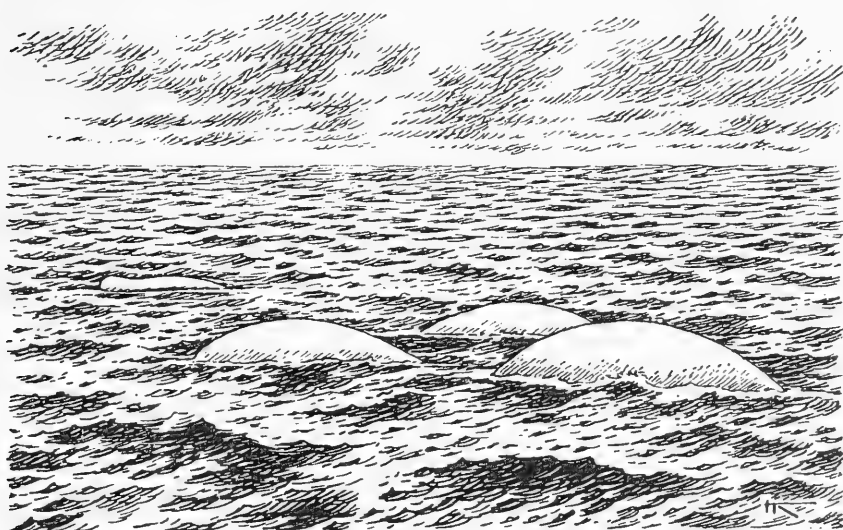


Fig. 334. A group of belugas at sea (figure by N.N. Kondakov).

Belugas feeding predominantly on pelagic life usually do not submerge deeper than 8-10 m. In any case, a herd surrounded by a sweep net usually does not escape from the lower edge even when the height of the net does not exceed 5 m and falls short of reaching the bottom. It is quite possible, however, that should the need arise, the beluga could submerge to several tens of meters. During feeding, belugas dive for 3-5 min but can remain submerged up to 15 min. After relatively long submergences in search of food, they surface three or four times in a row. Migrating animals surface regularly at 20-40 sec intervals with inhalation/exhalation extending for about a second while the back of the animal can be seen above the water for about four seconds.

While surfacing, the first to be seen above the water is the upper part of the head with the blowhole. The head is then submerged as the dorsum arcs above the sea surface. This semicircle, moving around its own axis, gradually disappears under water. Caudal flukes are never displayed. The blow is rapid, like a small bush, and is seen like a white flash in sunny weather (V.A. Arsen'ev).

The beluga does not avoid ice. In the north and the Far East, at places of its summer habitation, it is seen on days when the ice is broken and the animal remains free for the first time between ice chunks. In the north the beluga is common along the edges of ice and seen quite often in air holes (in the ice) and open water pools among drifting ice up to 9 to 10 points in density. In such cases, small herds are more common. The animals can overcome considerable masses of dense, apparently compact ice, past which they enter the open water in which their food is concentrated. Such instances are common in the Shantarsk archipelago in the Sea of Okhotsk. Instances are known of encountering small groups of belugas in large air holes among stationary ice in which they sometimes even winter.

The beluga does not avoid freshened or even fresh water. In the freshening waters of the estuaries of large rivers, belugas are regularly seen and are hunted. Almost all over the range, dozens of large and small rivers are known in which the animals regularly transgress chasing fish. In most cases, they rise up along the river for several tens of kilometers and are seen quite often even at a distance of 100-200 km from the estuary. In some large rivers, these animals were sighted at a very long distance away from the estuary: in the Yenisey almost near Podkamennaya Tunguska at over 800 km, in the Amur at Khabarov at about 1,000 km, in the Pechora at 900 km, in the Ob' at 1,500 km, and in the Yukon almost at 1,500 km.

Vision and audition are well developed in the beluga but the former is effective only at a close distance. The animals can orientate themselves

in many situations through their sense of hearing. They can perceive various sounds, including those produced in a very wide range by other belugas. These sounds are in the form of clicks and creaks and various types of whistles; they also resemble barking, roaring, and gnashing, and a sound somewhat similar to a trill. The sound frequency varies from a few kHz to 10,000 and even 20,000 kHz. Sounds play the role of various signals and are used for echolocation. Hunters well know that if even one beluga finds an exit from the net surrounding the animals, the entire herd escapes through that very exit in a very short time. It is also known that the animals well perceive all the sounds produced not only in water, but also in air (on the coast or on the ice). Moreover, belugas can very well orientate themselves to sea-level changes (high and low tides) and are almost never cast on the coast (Arsen'ev, 1939; Tomilin, 1962; Kleinenberg *et al.*, 1964).

Experiments in raising the beluga in an aquarium have yielded positive results. A male survived in an aquarium for several years and was taught during this time many "acts" of a "dolphin circus". This, together with the external appeal of this white whale, was greatly appreciated by numerous visitors to the aquarium.

Seasonal migrations and transgressions. Large regular migrations represent a characteristic feature of the biology of the beluga. However, the periods and courses of migration of individual populations have been studied very schematically and opinions are often contradictory.

White Sea. The beluga is generally seen at May end to early June after the sea becomes free from ice. In the northern portion, mainly along the west coasts of Kanin Peninsula, it has been sighted even earlier, early in April, but such instances are generally rare and the herds few. In summer the beluga is encountered regularly almost all along the entire coast of the sea; it is most numerous in the Dvina and Onega bay's and along the west coast of Kanin. In August, the number of belugas begins to decrease and by October most of the herd goes into the Barents Sea (Klumov, 1936; Provorov, 1957). Some belugas overwinter in the White Sea, as can be seen mainly in the Kandalaksha and Dvina bays and also in the air holes in Voronka and Gorlo regions. From the air individual animals or small groups were sighted in winter among dense drifting ice in the central part and in Voronka (Khuzin, 1960; Kleinenberg *et al.*, 1964). Thus the bulk of the White Sea beluga population inhabits the White Sea from early spring to late autumn, then enters the Barents Sea before its total freezing, where, apparently, they winter in its southeastern section. Spring migrations of animals commence as soon as the icy environment permits, sometimes even when a large part

of the sea is packed with dense drifting ice. In summer belugas are distributed throughout the sea and transgress into the numerous gulfs and bays (Klumov, 1934; Provorov, 1957).

Barents Sea. A small number of belugas is seen throughout the winter at different places along the Murman coast, which they probably abandon in March. The beluga remains in the region of Kolguev Island and the Chesha Bay throughout the year: in winter, in open water pools and along the edges of ice, moving toward the coasts in summer. In the region of Vaigach Island and along the west coast of the southern island of Novaya Zemlya, belugas are most numerous early in winter but, when the ice recedes, herds of belugas are seen close to Novaya Zemlya throughout winter and even in spring. Early in summer large-scale migrations of animals into the Kara Sea are noticed through the strait as also around the northern extremity of Novaya Zemlya. By mid-July, belugas have almost disappeared from the western coasts of these islands. In autumn large herds of belugas are once again seen here, now moving in westerly and southwesterly directions.

At the end of June herds of belugas are seen in the straits and bays of Franz Josef Land archipelago, where they remain until autumn but disappear again with the formation of an ice cover (Klumov, 1936a; Kleinenberg *et al.*, 1964).

Thus belugas arriving from the White and Kara seas winter in the Barents Sea. They live along the edges of drifting ice in the region of Kolguev Island—Chesha Bay and also along the western coast of Novaya Zemlya depending on ice cover conditions. Small individual herds of belugas move toward the Murman coast. At the beginning of summer, most of the animals leave the Barents Sea for summer feeding in the Kara and White seas. Some small herds remain throughout the year in different regions of the sea (Chesha Bay—Kolguev Island; southern part
575 of Novaya Zemlya—Vaigach Island; Franz Josef Land archipelago); for wintering, they go beyond the edge of ice or inhabit open water pools.

Kara Sea. Herds of belugas are seen in Kara Strait and in Yugorsk Shar Strait from the middle to the end of May and even in early June and travel into Baydarata Bay. At this time the animals enter the Kara Sea and encircle Cape Zhelaniya (northern tip of Novaya Zemlya). In some years the periods of movement of belugas vary considerably depending on the ice situation; further, in some cases, belugas were sighted even in April. In June, in Amderma region (east of Yugorsk Shar Strait), large herds of belugas move eastward and some are seen along the southeastern coast of Novaya Zemlya throughout July. Belugas reach the estuary of the Gulf of Ob early in July. On entering the gulf, the animals generally travel along the right bank since the prevailing northeastern winds

press the ice toward the left bank. Belugas return from the gulf mostly along the left bank or along the midsection of the bay. The Gulf of Ob, mainly at the point of its confluence with Tazovsk Inlet, belugas remain until the formation of an ice cover, i.e., until early November (Dukhovnyi, 1933, 1934; Chapskii, 1937; Kleinenberg *et al.*, 1964).

In the estuary of Yenisey Gulf, belugas are seen in the first few days of June (waters of Dickson Island) and even earlier in years of little snow. In most cases, herds of belugas arrive there from the east, from Pyasinsk Bay, and sometimes from the side of the open sea. Later, the animals remain there regularly and enter Yenisey Gulf and sometimes rise high up along the Yenisey River. In the strait, belugas traverse mainly along the eastern coast. In the September the number of animals decreases but individual herds are seen here throughout this months. In the second half of July and in August, belugas are common along the coasts of Pyasinsk Bay and are sighted quite regularly in August and September in Vil'kitskiy Strait and along the coasts of Severnaya Zemlya where en masse arrivals of arctic cod occur at this time (Heptner, 1930; Zikov, 1934; Klumov, 1936a; Kovalev, 1938; Kleinenberg, Bel'kovich, and Yablokov, 1960).

The migrations of belugas in the Kara Sea can be sketched as follows. In spring and early summer herds of belugas enter the Kara Sea through Novaya Zemlya Strait and around its northern extremity. The animals moving through the strait are seen in Baydarata Bay, later move eastward, and reach the Gulf of Ob by mid-July. By this time Matochkin Shar Strait has become ice-free and animals passing through this strait are seen along the eastern coasts of Novaya Zemlya from where, perhaps in part, they move also toward the southern coasts of the Kara Sea. The animals encircling Novaya Zemlya move eastward along the edges of drifting ice or along open water pools. Some move toward Severnaya Zemlya islands and others reach the mainland coast somewhere north-east of Pyasinsk Bay. These belugas, moving southwest later, are seen in Pyasinsk Bay, around Dickson Island, and in Yenisey Gulf; however, the animals sometimes reach Dickson Island not from the northeast, but from the north. Later, this group of belugas disperses and the animals are sighted along the coasts of Taimyr and in Vil'kitskiy Strait. In August and September and in years of little snow even in October, herds of belugas depart by the same routes (in a reverse direction) to the wintering sites. Therefore, the autumn courses of belugas in the estuary of Yenisey Gulf have a northeasterly direction and in the Gulf of Ob a westerly direction. Small herds of belugas winter in the Kara Sea, probably regularly, in the air holes in the Gulf of Ob and Yenisey Gulf, and in the large air holes among drifting ice in various parts of the Kara Sea.

The periods of migrations of belugas in the Kara Sea depend primarily on the period and concentration of the arctic cod, which represents the main food of belugas. Many major rivers enter the Kara Sea and bring with them masses of warm water in spring and summer. These waters, 576 rich in biogenic elements, promote the growth of phyto- and zooplankton and thus provide extremely favorable conditions for the habitation of the arctic cod, in search of which herds of belugas follow. Thus the periods and magnitude of arrival and distribution of belugas depend to some extent on the magnitude and distribution of river waters in the Kara Sea (Tarasevich, 1960a, 1960b).

L a p t e v S e a. The distribution and migrations of belugas in this sea are not quite clear. Herds of belugas (sometimes large ones) have been sighted in Vil'kitskiy Strait, along Cape Chelyuskin, in Pronchishcheva Bay, in Khatanga Gulf, in the estuaries of the Anabar and Olenek rivers, in the Lena delta, near Tiksi and, what is more, belugas have been sighted every day at some of these points. Thus the animals inhabit the entire southwestern coast of the Laptev Sea and sometimes herds of belugas are seen in July to September along the west coasts of Lyakhovsk and Kotel'nyi Islands (Klumov, 1936a; Kleinenberg, Bel'kovich, and Yablokov, 1960).

In all probability, an isolated but comparatively small population of belugas resides in the Laptev Sea and spends the winter in the large open water pools and air holes of this shallow water basin. In the summer months the animals inhabit the southern and western coasts of the sea including Vil'kitskiy Strait, Severnaya Zemlya coast, and possibly the adjoining Kara Sea waters. During their habitation in the waters of Novosibirsk Islands, belugas are sometimes seen in adjoining regions of the East Siberian Sea. Late in autumn the animals leave the coasts for the central part of the sea where they winter.

S e a o f O k h o t s k. The maximum collection of belugas in summer is seen in the western (Gulf of Sakhalin, Amur liman, and Shantarsk archipelago) and northeastern (Shelikhov Gulf with Penzhina and Gizhaga bays) parts of the sea. In the northwestern part of the sea, from Shantarsk Island to the region of Ayan-Okhotsk and along the western coast of Kamchatka, belugas are encountered in small numbers. They have not been noticed in the central deep water portion of the sea. Probably, two local herds of belugas spend the summer in the Sea of Okhotsk and could be called Amur and Penzhina herds (Arsen'ev, 1939).

The earliest appearance of large beluga herds in the southwestern part of the Sea of Okhotsk (evidently in April) was recorded in Terpeniya Bay along the southeastern coast of Sakhalin (Polyakov, 1884). At the

end of April to early May, small numbers of animals arrive in Tatar Strait where they remain on the edges of stationary ice in the northern section of the strait. Early in May many belugas are sighted in the narrow part of Tatar Strait (Pogibi-Lazarev) and the animals approach the coasts as soon as the ice breaks up along Sakhalin. As the strait becomes clear, belugas gradually move northward into the Amur estuary but are confined to the narrow part of the strait generally up to mid-July, leaving only after the fish (herring and humpback salmon) disappear there. The animals then move into the Amur estuary and into Sakhalin Strait.

Concurrently, at May end to early June, large herds of belugas approach from the southeast to the northern extremity of Sakhalin and, encircling the island from the north, reach the Gulf of Sakhalin, most of which at this time is still covered by compact ice. On the Sakhalin coast of the bay, ice begins to break in the first half of June and herds of belugas are seen immediately thereafter in the Gulf of Sakhalin and later in the Amur estuary. These animals live there until late autumn.

Roughly at the same time (or slightly later), belugas are seen in the bays of the Shantarsk Sea while the sea itself and partly the large gulfs are still ice-bound. However, the dense drifting ice is no obstacle to the belugas moving in the upper courses of the bays which are free of ice (Tugursk, Ul'bansk, and so on).

The migrations of Amur belugas can be sketched as follows. In April-May, herds of belugas appear in Terpeniya Bay and later a part of this herd moves through La Perouse Strait into Tatar Strait and feeds in its
 577 northern section on herring and humpback salmon. By mid-July, belugas leave for the Amur estuary and the Gulf of Sakhalin. Almost concurrently, at the end of May, most of the herds approach the northern extremity of Sakhalin from the southeast, encircle Sakhalin from the north, enter the Gulf of Sakhalin, and later Amur estuary in the first ten days of June. Here the animals feed throughout the summer. Roughly at the same time, a part of the herd from the northern extremity of Sakhalin turns not into the Gulf of Sakhalin, but moves west and arrives in the large bays of the Shantarsk Sea over large masses of dense ice. There they are encountered throughout July, August, and September. Individual small herds may arrive from the Shantarsk Sea along the coasts in the northeast and are sometimes seen in the region of Ayan Bay. Some animals may even reach the estuaries of Okhota and Kukhtui rivers.

The nature of migrations of belugas changes in autumn. Instead of large compact herds, small isolated groups scattered over a large water body are seen. With the formation of a compact ice cover at the end of October-November, belugas abandon points of summer habitation. A small part of the herd arrives October end or early November from the

north into Tatar Strait and apparently exits through La Perouse Strait into the Sea of Okhotsk. Most of the herd from the Shantarsk Sea and the Gulf of Sakhalin encircle Sakhalin from the north at October end and in November and head southeasterly. During autumn migrations very large herds are not seen. The periods of migrations cover a long time frame. Probably, with the disappearance of schooling fish, some animals begin to leave the summer feeding waters even before ice formation; formation of dense or stationary ice cover then compels the remaining animals to leave. The wintering sites of belugas have not been established (Dorofeev and Klumov, 1936a; Arsen'ev, 1939).

According to the latest observations, groups of belugas have been recorded north of Sakhalin in winter in air holes among dense drifting ice (G.A. Fedoseev). It is possible that some herds spend winter amidst ice in the midpart of the Sea of Okhotsk.

In Penzhina and Gizhaga bays of Shelikhov Gulf, belugas are seen close to the coasts at the end of May immediately after the thawing of coastal fast ice in the bays and gulfs. The animals remain there throughout summer feeding on schooling fish (herring and salmon). They perform regular local migrations, their periods and directions depending on the powerful low and high tides (at some points during low tide, the coast is exposed for a distance of 5 km or more). Belugas inhabiting Shelikhov Gulf reach west up to Tauy Bay and some animals or small groups have been encountered even more westward, right up to Okhotsk. A few animals are encountered in the summer months along the west coast of Kamchatka (predominantly in its northern section). With the appearance of floating anchor ice and the subsequent freezing of coastal waters in October-November, belugas leave the coasts and are no longer seen in these waters in the winter months (Arsen'ev, 1939). The points of wintering of this herd of belugas and the courses of their migrations have not been established. The winter ice cover of Shelikhov Gulf is typical. Thus in Gizhaga Bay coastal shore ice 20-25 miles wide is formed while the midpart of the gulf is covered with drifting ice. In Penzhina Bay only small straits freeze while the entire remaining water body is covered by floating ice of varying density. It is quite possible that herds of belugas may winter in the regions of sparse ice without undertaking distant migrations. There are, however, no observations on winter movements.

Migrations of belugas in the Bering and Chukchi seas have been very poorly studied. In summer the animals concentrate in the Gulf of Anadyr and the Anadyr estuary. Many schooling fish entering this river serve as food for the belugas and hence beluga arrivals are often en masse.

Belugas are seen scattered throughout this bay in July. At about this time also, belugas are seen at many points in the Chukchi Sea: Cape Serdtse

Kamen', Kolyuchin Inlet, Cape Shmidt, and probably somewhat later on Wrangel Island and north of it (up to 72 to 73° N lat.). Simultaneously they are also seen on the coasts of Alaska where they are known from Bristol Bay to at least Cape Barrow. In Bering Strait, spring (April-May) migrations of belugas occur in the north while autumn migrations (September-October) are observed in the south (Arsen'ev, 1939; Nikulin, 1946).

The migrations of belugas in these waters can tentatively be described as follows. The animals winter in the eastern and northeastern parts of the Bering Sea. In April-May, with the disappearance of ice, they begin to move north and northwest. Some belugas exit into the Chukchi Sea and are distributed over an immense water body, from the boundaries of the East Siberian Sea to Beaufort Sea and Wrangel Island, depending on the disposition and density of ice. Other, probably more, animals remain at the inlet into the Gulf of Anadyr and with thawing of ice, are scattered over this water body, where they spend the summer months. In autumn (October-November), with the compaction of ice and the formation of young ice, animals from the Chukchi Sea move southward, cross Bering Strait, and leave for their wintering sites. The ice displaces the belugas from the Gulf of Anadyr also, compelling them to move east and southeast.

In most cases, the dispersal of migrating marine mammals (whales, belugas, and walruses) in the Chukchi Sea is restricted in the west by the line Cape Shmidt—Wrangel Island since De Long Strait almost year-round is covered by a broad strip of very dense ice (Arsen'ev, 1935). On encountering this massive ice obstacle, the animals change course northward toward Wrangel Island and travel farther west into the waters of the East Siberian Sea only in years of little ice.

In winter months belugas are noticed at many points in the Bering and Chukchi seas, where they remain in large air holes and open water pools formed among the floating ice. Wintering belugas are noticed almost every year close to Provideniya Bay (northeastern part of the Gulf of Anadyr); animals are sighted at different points along the coast of the Chukchi Sea: Nunyamo, Lesovsk, Dezhnev, Serdtse-Kamen', and other capes (Nikulin, 1951; Uspenskii, 1958; Kleinenberg *et al.*, 1964).

In the Beaufort Sea, belugas are encountered in summer in Amundsen Gulf and McClure Strait, to the west of Banks Island, at many points in the MacKenzie delta, and to the west of the estuary of this river. It has been suggested that, in the Beaufort Sea, belugas even winter far from the coasts since they are seen in spring concurrently at many points (Vladykov, 1944; Sergeant, 1962a).

In the eastern part of the Canadian Arctic, belugas similarly undertake seasonal migrations, which are most distinctly manifest in Davis Strait and Baffin Bay. In summer they sometimes reach 80°N lat. (Hall Basin), descending in winter to the middle of Davis Strait: Cumberland Sound—Sukkertoppen. Regular migrations in spring and autumn are noticed in Hudson Strait but a small number of belugas winters in the western and northern sections of Hudson Strait, eastern part of Cumberland Sound, and in Lancaster and Jones sounds. In the Gulf of St. Lawrence, as it frees from ice, belugas are seen in the estuary of the river (often transgressing into the river) and at other points on the coast but abandon these regions in autumn.

The population living east of Greenland probably overwinters to the north and northwest of Iceland. In spring the animals migrate northward, reaching Spitsbergen, often in large numbers, and return to the wintering sites in autumn (Vladykov, 1944; Daan and Douglas, 1953; Sergeant, 1962a).

Transgressions of belugas beyond the limits of their normal range are not very rare. In the Bering Sea, belugas were noticed in the waters of Karagin (58°N lat.) and Commander Islands (54°N lat.) (Tomilin, 1957) although 46°N lat. serves roughly as the southern boundary of the distribution of belugas in the Sea of Okhotsk. From the Chukchi Sea some animals or small groups reach the estuary of the Kolyma and the central part of the East Siberian Sea, although they may reach there later from the Novosibirsk Islands. Animals of the two populations may be encountered there.

Transgressions into the Atlantic Ocean usually occur in particularly cold winters. In the western part of the North Atlantic, the southernmost transgression was noticed in Massachusetts Bay (42°N lat.) and in the eastern part along the coasts of Great Britain, Holland, Schleswig coasts in the Baltic Sea, Estonia, Finland, and even France (von den Brin, 1958; Kleinenberg *et al.*, 1964). During 1964 to 1966, eleven sightings of belugas were recorded in the waters of Central Europe. The well-known case of the long residence of a beluga in the Rhine is particularly interesting. Close to Nijmegen town, Holland, a beluga was sighted on May 18, 1966. Gradually, ascending against the current, it crossed Deventer, Kampen, Duisburg, Dusseldorf, and Bonn, and on June 13 reached Honnef, which is 400 km from the sea (50° 40' S lat.). Here the beluga turned back and entered the sea on June 18 after moving downstream for 400 km in five days. Attempts to catch it in a net or by roping or using an injector gun were not successful. This adult beluga with a body length (visual) of 5 to 6 m spent a month in fresh water, which is rather unusual (Slijper, 1967).

Reproduction. In the Sea of Okhotsk mating of belugas was recorded in April-May (Nikol'skii, 1936); in the Gulf of Ob in July (Zaikov, 1934); in the Barents and Kara seas from May through August, peaking in May-early July (Kleinenberg and Yablokov, 1960); in the Gulf of St. Lawrence from February to August with a large number of animals mating in May and June (Vladykov, 1944); and in Hudson Bay from March through September, peaking in May (Daan and Douglas, 1953). Thus the period of mating extends for about six months but the majority of females are fertilized over a relatively short duration, i.e., from April end to early May. Only some individual animals mate at other times.

In the White Sea, calves with the umbilical cord intact were encountered in mid-July (Provorov, 1957) in the Gulf of Ob (Zaikov, 1934), in Hudson Bay (Daan and Douglas, 1953) on August 15, and in the Sea of Okhotsk from July 18 to 26 (Kleinenberg *et al.*, 1964). However, judging from the dimensions of the suckling calves caught in the summer months, their births may have taken place much earlier (Kleinenberg *et al.*, 1964). In all probability, the period of parturition, like the period of mating, is protracted and births may occur from early spring throughout the summer months. The period of maximum births has not been ascertained. Thus gestation in belugas extends for 11-12 months and, according to one view, might be extended 13-14 months (Sergeant, 1962a).

Information on the duration of lactation is quite contradictory, from 5-6 months to 12 months or even longer. Until the end of September (close of the hunting season and specimen collection), calves were found feeding exclusively on milk. In the stomach of animals of the next color stage, i.e., gray belugas, milk was also found together with food gathered independently, but the age of these animals could not be established. It would probably be more correct to assume that the period of lactation extends for six months (Kleinenberg *et al.*, 1964). At the same time, the teeth of young belugas emerge roughly at 10 months of age and hence it is possible that milk suckling of the calves ceases in this period.

The female usually delivers a single calf although, as among other cetaceans, twins are sometimes encountered. One female contained three embryos (two males and one female). It has been suggested that female belugas are capable of mating at a short interval (two to four weeks) after parturition. This suggests the possibility of annual births but investigations carried out on various beluga populations have shown that some percentage of mature females do remain barren every season. The ratio between barren and gestating females in a herd varies considerably in different years as also in different regions of habitation. It has not been possible to establish the pattern of barrenness and hence the reproduction cycle of this animal can only be surmised. In some cases, it appears

probable that a female may give birth for five to six or more consecutive years, after which she rests for a year (or more). In other cases, such rest periods might set in after two or three years (Tomilin, 1962; Kleinenberg *et al.*, 1964). It is also possible that the reproduction cycle varies for females of different age groups. Therefore, the tempo of population replenishment has yet to be established and recommendations for the rational commercial exploitation of the beluga are difficult to make.

In the period of mating it was sometimes observed that two or more males chased a single female while groups of 10-20 adult males, isolated from mixed groups, were encountered concurrently. This suggests the possibility of polygamy among belugas (Sergeant, 1962a).

Growth and development. Measurements of beluga embryos from Greenland waters showed that in the period of embryonal growth, development is relatively uniform (Table 53).

Since the period of births is very prolonged, embryos of different size may be encountered at any time of the year (Fig. 335). Thus in the northern seas of the Soviet Union, the length of measured embryos varied from 7 to 168 cm, the embryos investigated in July being larger than those found in August and September (Kleinenberg and Yablokov, 1960). The maximum dimensions of embryos differ in different regions of the species' range. In the Kara Sea, the largest embryo was 150 cm long, in Hudson Bay 151 cm, Barents Sea 170 cm, Sea of Okhotsk 175 cm, waters of western Greenland 183 cm, and in the Gulf of St. Lawrence 213 cm. Newborn calves are often smaller than the larger embryos. Thus the length of the smallest calves (from among those measured) was (in cm): in western Greenland 116; Sea of Okhotsk 130; Kara Sea 140; Barents Sea 147; Gulf of St. Lawrence 147; and Hudson Bay 153. The average body length of a newborn calf, covering all the regions, is assumed to be 150 cm (Kleinenberg *et al.*, 1964).

The growth rate of belugas is the highest in their first year. The average monthly increment has been put at 30 cm; in the lactation period

Table 53. Body length of beluga embryos, cm (Nielson and Dagerbol, 1930; after Tomilin, 1957)

Month	Number of specimens	Body length	Average
November	36	32-78	60.2
December	40	46-104	87.3
January	11	88-112	96.3
February	19	122-142	129.9
March	19	113-183	142.2
April	6	142-158	149.1

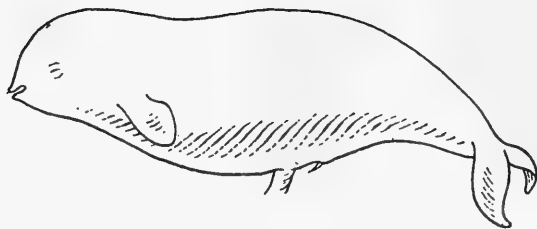


Fig. 335. Embryo of beluga (figure by N.N. Kondakov).

the increment should be more than after changing over to independent feeding. By the end of the first year the animal reaches a length of almost 300 cm. The dimensions of belugas at the age of up to one year from the Sea of Okhotsk varied from 140 to 280 cm, the peak of the growth graph falling in the 180-200 cm interval.

Further growth of belugas is identified from the color changes of the
 581 animals in three stages. Animals of the first color group, called "gray" animals, have a bluish-gray body and are immature. The next color group, the "blue" group, covers animals transiting from gray to white. Mature as well as immature animals of both sexes are encountered in this group. Finally, the "white" group comprises adult mature animals of various sizes with a pure white body color. The age of transition from one color group to another has not been established.

It has been assumed that the average annual increment in the second and third years is 75 cm and in the fourth year about 45 cm among males and about 30 cm among females (Sergeant, 1959a). The males soon outgrow females and hence the average size of adult males is more than that of females (Table 54).

Age determinations of females based on dentine layers in the teeth showed that the immature group comprised animals of three to four years (body length 202-317 cm) but females aged two to five years could be placed in the group of potentially mature animals. The minimum age of mature females is three years but the maximum number of northern belugas mature at age four to five years or more (body length 315-435 cm). Among mature belugas, the growth rate decreases sharply. In the first year after sexual maturity, the female adds an average of 20 cm, in the second year 5-7 cm, and in the third year 2-3 cm. In the fourth to the fifth years of maturity, growth ceases and the animals attain physical maturity. By then, they measure 355-360 cm in body length and fall in the age group seven to nine years. The body length of females in the Far East in the first year of maturity rose by 28 cm, in the second and third years by 7-9 cm, and in the fourth and fifth years by 2-4 cm. Their

Table 54. Body dimensions of belugas of different color groups, cm (Kleinenberg *et al.*, 1964)

Region	Color group	Males			Females		
		Number of specimens	Body length	Average	Number of specimens	Body length	Average
Gulf of St. Lawrence	Gray	8	226-263	247	13	203-282	239
	Blue	12	282-345	311	18	282-343	318
	White	59	329-447	406	38	310-409	372
Kara Sea	Gray	7	239-340	276	15	224-341	272
	Blue	20	300-393	336	17	274-365	322
	White	35	343-472	400	26	326-390	353
Sea of Okhotsk	Gray	34	195-310	252	28	170-357	286
	Blue	173	187-479	351	98	257-422	331
	White	136	359-500	447	53	360-418	388

physical maturity set in in the fifth to the sixth year after sexual maturity. The average body length of physically mature females in the Far East was 390 cm (Kleinenberg *et al.*, 1964).

Male belugas from Hudson Bay attain sexual maturity at six to nine years (12-18 dentine layers) at a body length of 275-320 cm and females at six years (12 layers) at a body length of 275 cm. Belugas on the eve of the "white" stage have 13 to 18 dentine layers. Up to 35 layers are seen in very old animals. The maximum number of layers counted is 50 (Sergeant, 1959a). Longevity of the belugas has not been established.

Enemies, diseases, parasites, mortality, and competitors. The killer whale and the white polar bear may be regarded as enemies of the beluga albeit they inflict little damage on the population. Apart from diseases caused by parasites, no other has been recorded. Ectoparasites are not known.

Thirteen species of helminths are known among belugas: trematodes three, cestodes one, nematodes eight, and acanthocephalans one. None of the three species of trematodes has been reported in any other animal. The trematode *Odneriella seymouri* Price was found in the Bering, Okhotsk, White, and Barents seas. *Leucasiella arctica* Delamure and Kleinenberg, parasitizing the rectum, has been detected in the Barents Sea. *Leucassiella mironovi* Krotov and Delamure was found in the small intestine of belugas from Aniv Bay and La Perouse Strait.

The cestode *Diphyllbothrium lanceolatum* Krabbe, reported before for three or four species of pinnipeds and possibly common porpoises, is evidently a facultative parasite of the beluga.

Four of the eight known species of nematodes have been exclusively reported in the beluga. *Anisakis* (*Anisakis*) *kükenthalii* Cobb, parasitizing

the stomach, was found in the Arctic Ocean (Spitsbergen), the Barents, Kara, North, and Okhotsk seas, and in Aniva Bay (Sakhalin). *Stenurus arctomarinus* Delamure and Kleinenberg was detected in the lungs of belugas from the northern Arctic Ocean, and White and Barents seas. *Otophocaenurus oserskoi* Skrjabin, localizing in the auditory organs, was found among belugas from the waters of Sakhalin, northern Arctic Ocean, and White and Barents seas. *Stenurus pallasii* van Beneden, parasitizing the auditory organs, bronchi, and circulatory system, was detected in the Arctic. *Anisakis (Anisakis) simplex* Rudolphi, very widely distributed among marine mammals, was found in the gullet, stomach, and intestine of belugas and also in ten other species of toothed whales, two species of baleen whales, and Steller's sea lion. It is known from various places in the North Sea, eastern Kamchatka, Japan, and New Zealand. *Terranova decipiens* Krabbe, parasitizing the stomach and intestine, has been detected in the beluga only once (Kara Sea), whereas it occurs in 12 species of pinnipeds, 2 species of toothed whales, and 2 species of baleen whales in the North Sea, the Atlantic and Pacific oceans, and in Antarctica. The nematode *Stenurus minor* Kühn, found among belugas in the northern Arctic Ocean, North Atlantic, North, Black, and Azov seas, and along the Asian coast of the Pacific Ocean, parasitizes the auditory organs, bronchi, heart, and blood vessels of only common porpoises in addition to the beluga. Finally, *Crassicauda giliakiana* Skrjabin and Andreeva parasitizes the same organs of the beluga and common porpoise. It has been detected in the Amur estuary and in the waters of Kuril Islands.

The lone species of acanthocephalan parasitizing the intestine of beluga, *Corynosoma strumosum* Rudolphi, is known in 11 other species and subspecies of pinnipeds, common porpoises, the sea otter, and also land carnivores and ichthyophagous birds. Among marine mammals, this helminth has been found along the Atlantic coast of Europe, in the Baltic Sea, Lake Ladoga, along the Canadian coasts, in almost all the northern waters of the USSR, around the Kuril Islands, in the waters of Sakhalin, along the coasts of California, and in the Caspian Sea (Delamure, 1955; Tomilin, 1962).

Population dynamics. Changes of beluga populations relative to natural factors are not known. The comparatively low scale of hunting perhaps does not influence the numbers of this species.

Field characteristics. The pure white color of adult animals distinguishes this species from all other marine mammals. Further, the beluga has no dorsal fin. The corpus adiposum [melon] is prominent, reaching almost the end of the broad snout; a "beak" is absent. The teeth are conical and develop in both jaws; canines are absent. In all the color

groups, coloration is monochromatic. Belugas usually stay together in groups which gather into herds of various strengths. In the period of en masse arrival of fish which serve as their food, belugas form herds of thousands of animals. This species is essentially a coastal form but is also encountered amidst ice at times of high density. (V.A.)

Economic Importance

583 Although beluga hunting has been carried out for several centuries in our country, it has never been extensive. In the 1920s to the 1930s, beluga hunting in the seas of the Soviet north and Far East expanded but was not intensive. In the years of maximum catch (1931-1935), the number caught in the Soviet Union did not exceed 5,000. The maximum catch occurred in the Far East up to 1940 but thereafter dropped to a few hundreds per year. After 1950, hunting intensified somewhat in the White, Barents, and Kara seas, but nonetheless the annual catch has never exceeded a couple thousand animals. Outside the limits of our waters beluga hunting is also not significant. Formerly, the most productive area was the Gulf of St. Lawrence where some 2,000 belugas were caught annually, dropping to a few hundreds in 1932-1938; hunting ceased altogether in 1940. In Hudson Bay, from 1948-1960 more than 1,000 belugas were caught only in three years, the catch varying from 600 to 900 in the other years. In the waters of Greenland and Spitsbergen, the annual catch used to vary widely, from a few tens to several hundreds. In the rest of the Canadian Arctic regions, the catch was invariably low. Statistics of beluga hunting are far from perfect and the figures cited should be regarded as highly tentative. Nevertheless, the catch of beluga throughout its range has never been much and hence the products of beluga hunting have never been of commercial or economic importance.

The techniques of catching the beluga are diverse and specific to each region. The oldest equipment for catching the beluga in the European north is the White Sea sweep net whose length depends on the capability of the cooperative (number of operators and karbases* available) and may go up to almost 2,500 m. In principle, this is a dynamic method of catching but is extremely primitive in practice. A composite net 2,400 m long is cast in the open sea, not farther than 7 to 8 km from the coast; the operation involves 24 boats and 170 people. The depth of casting should not exceed the wall height of the sweep net. Two sections each of the net set up on two boats are stitched together before setting out to catch and these boats enter the sea in pairs. Such pairs are

* Large boats with high sides used in marine and river transport—Translator.

deployed at some distance from each other in a semicircle open on the side of the anticipated approach of the herd of belugas. As the animals enter this semicircle, each pair of boats begins to diverge in the opposite direction, casting the sweep net into the water and joining it with the successive pairs to ultimately form a circle with the sweep net. This circle is gradually closed, its diameter reduced, and the boats enter the circle of the sweep net. The belugas are killed from the boats by shooting or battering with ice chisels. The killed animals are towed to the coast and dressed. The production cost of hunting by this method is extremely high (Klumov, 1936b, 1939).

Another, much older piece of equipment used in catching is the Norwegian stationary net. Its wall height varies from 8 to 14 m and length 450 to 1,200 m. The net is set up only at places of regular arrivals of belugas at an angle of 30 to 35° to the coastline. A brigade of catchers consists of 8 to 12 persons with some boats. The men in the boats approach the beluga herds from the sea side and attempt to chase the animals into the net inlet by raising a racket, after which the inlet is sealed by a net. The belugas trapped within the net are battered with ice chisels and dragged to the coast (Heptner, 1930).

The fabric mesh or so-called "polovinka" [meaning half] is similarly passé. Its length is 25-50 m, height 8-12 m, and mesh size 50-60 cm. These nets are set up on anchors perpendicular to the coast in a checkered pattern at a distance of not less than 15 m from each other. The lower seine rope should reach the bottom. A team of five persons can operate 30 to 40 such "polovinkas". The animal passes through the mesh but its caudal fin becomes entangled and the net twists around it. With no possibility of floating, the animal succumbs to asphyxiation. Best results are obtained on dark autumn nights when the belugas cannot see the net (Klumov, 1939). These traps have been modernized in recent years, with plant fiber replaced by capron [nylon] or flexible galvanized steel cables, 584 which are less visible in the water. Hunting is done in the open sea from a ship (in the region of Novaya Zemlya and in Yenisey Strait), which chases a herd of belugas into the net. Such innovations have significantly increased the catch in such traps (Butorin, 1957).

The development of beluga hunting in the Far East took a different course. The prototype of the beluga net here was an ordinary casting net used for catching salmon. Special coastal nets of this type, up to 1,000 m or more in length and made of thick strong material, were used for catching belugas. The ends of the net, laid on a kungas,* were affixed to the coast. As a herd approached, the boat with the kungas in tow

* Open fishing boat with a carrying capacity of 3-5 tons—General Editor.

surrounded it and drew the second end of the net to the coast. The net was then hauled in manually or with a winch to the coast and the captured belugas gradually removed, killed, and dressed (Fig. 336).

Later, this coastal net was elongated to 2,500 m and was gathered on two kungases standing together with two boats on anchors more than 1 km from the coast. As a beluga approached, the kungases were towed simultaneously in the opposite direction which hastened trapping of the animal and enlarged the area of catch. Both ends of the net were drawn to the coast and its further hauling in and removal of the animals done as in the coastal method of catching.

In the course of further modernization (I.K. Nepomnyashchii), a deep net was designed with a length of about 1,000 m and a wall height of 18 m. Using two boats and one kungas, a herd of belugas was surrounded comparatively far from the coast, the net with the caught belugas was towed to the coast, and the trapped animals were recovered from the large net by the conventional method. This did not make for venturing beyond 10 km from the coast, towing took several hours, and if the weather turned foul, there was danger of losing not only the catch, but the net itself. A new net 1,600 m in length with a wall height of 18 m was subsequently designed. It was cast from two motor boats without a kungas. On sighting a herd of belugas, these boats diverged in the

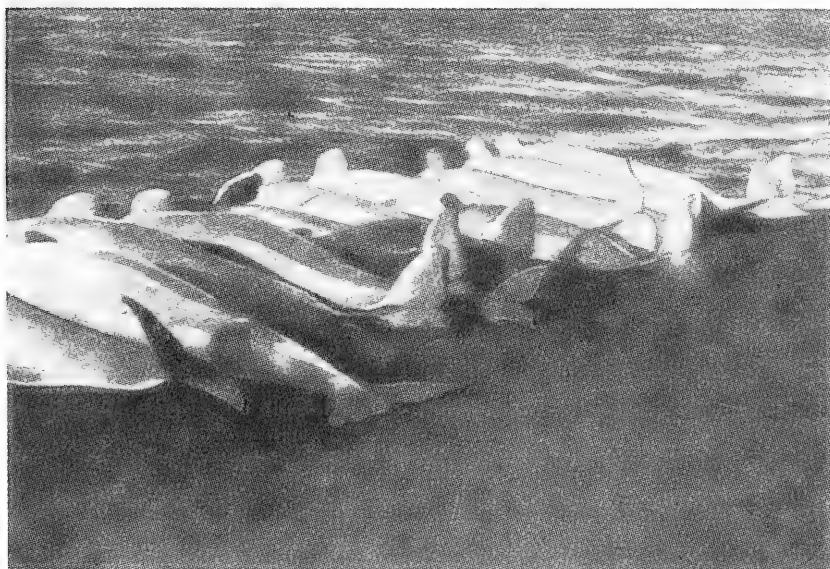


Fig. 336. Caught belugas laid out on the coast. Sakhalin, 1938 (photograph by V. A. Arsen'ev).

opposite direction and surrounded the herd with the net. After this, much of the net was gathered in so that a small circular section remained under the water. The boats, traveling in the opposite direction, gradually tautened and transformed this circular section into a line. The belugas caught in the net died of asphyxiation, were dragged to the approaching kungas, and hauled to the coast (Fig. 337). The team of catchers using these nets consisted of 25 to 30 persons (Arsen'ev, 1940).

At places with a high variation in sea level during low and high tides, the belugas trapped in the net were left until low tide set in and then dragged to the coast for killing and dressing.

The coastal people sometimes shoot belugas with rifles but many of the killed animals are lost. Sometimes the beluga is first harpooned manually and then shot. This method was in vogue for sometime in the Gulf of St. Lawrence and other regions of the Canadian Arctic. At some places the belugas are chased into narrow straits and the exit sealed off by a net. In most cases, these primitive methods of hunting result in a low catch.

In dressing the killed belugas, the subcutaneous fat layer together with the skin is removed first. The fat layer is later separated from the skin and oil obtained from the blubber. The skin, now free of fat, is salted and after a few days, the thick layer of epidermis recovered. The skin is again salted and, after sometime, packed in barrels for dispatch



Fig. 337. Towing the trapped belugas. Sakhalin, 1938 (photograph by V.A. Arsen'ev).

to leather manufacturers. The remaining carcass is processed into edible parts and those to be used in fertilizer meal. Where there are no processing facilities, the carcass is used as feed for fur-bearing animals. The oil melted from the blubber is used for commercial purposes. The oil from the head (corpus adiposum [melon]) and from the hollow of the lower jaw is collected separately. This oil possesses the property of remaining fluid at low temperatures and is used a special lubricant. The skin of the beluga can be used in making shoe soles and other footwear articles as well as halters and reins. Further, the intestine of the beluga can be satisfactorily used in the sausage industry; 30 m long, the intestine lengthens three times over after removal of the muscular layer. Blood accounts for roughly 5% of the overall weight of the animals. The valuable product,
 586 black albumin, can be produced from the blood (Dorofeev and Arsen'ev, 1936; Druker and Gakichko, 1936).

The average weight of males and females of different color groups of belugas are given in Table 55. Table 56 gives the weight of the body parts of some animals. The ratio of the weight of different body parts of belugas without classification into age (color) groups is shown in Table 57 (those sections of the carcass used commercially were weighed).

The beluga reserves in all the regions of its extensive range are not as large as often assumed and hence their catch should be based on a knowledge of the biology and population of these animals. Beluga hunting has been restricted in recent years but could be enlarged without affecting these reserves. This could be done first in the Far East seas where not more than a thousand belugas have been caught annually since the 1940s. In the northern seas the increase should be more cautiously approached since hunting here is already vigorous although the possibilities of commercial exploitation of the animal population have
 587 not been fully realized. It should not be forgotten, however, that in Hudson Bay, for example, some restrictions have been imposed on hunting since even the comparatively low catch over several years has reduced

586 Table 55. Average weight of whole animals from Sakhalin Bay, kg (Arsen'ev, 1935b)

Sex	Color group									
	White		Blue		Gray		Sucklings		Total	
	No.	Av. wt.	No.	Av. wt.	No.	Av. wt.	No.	Av. wt.	No.	Av. wt.
Males	120	880.1	38	489.4	21	310.4	2	150.0	181	726.2
Females	81	656.6	31	506.1	27	281.4	4	122.4	143	537.6
?	7	—	3	—	63	—	2	—	75	—
Total	208	789.7	72	494.3	111	266.5	8	122.9	399	577.4

586 **Table 56. Weight of body parts of belugas from Sakhalin Bay, kg (Druker and Gakichko, 1936)**

Body part	Color group of belugas					
	White			Blue		Gray
	1	2	3	1	2	1
Skin:						
Epidermis ("jacket")	34.5	—	28.2	26.5	24.6	14.2
Dermis	18.5	57.2	27.3	13.9	11.8	9.1
Fat of:						
Trunk	240.8	151.5	294.3	146.6	114.5	66.6
Head	4.1	7.5	10.9	4.1	2.8	1.4
Jaw	0.8	0.5	0.3	0.6	0.6	0.2
Flesh	242.2	184.4	217.4	208.6	155.7	58.6
Bones	68.2	77.2	86.0	65.3	37.3	25.3
Flippers	8.1	9.1	9.7	9.1	5.2	3.2
Caudal flukes	8.9	9.0	12.5	9.5	5.2	3.5
Viscera:						
Liver, heart, lungs, kidneys, and stomach	72.3	49.0	65.6	77.7	35.5	15.5
Intestine	22.6	16.0	18.1	19.0	11.5	5.5

587 **Table 57. Weight of carcass sections of belugas from Sakhalin Bay, kg (Dorofeev and Arsen'ev, 1936)**

Number of belugas	Av. wt. of one animal	Wt. of skin with fat and epidermis		Wt. of carcass without viscera		Wt. of skin and epidermis without fat		Wt. of skin without epidermis	
		Av. wt.	% of body wt.	Av. wt.	% of body wt.	Av. wt.	% of body wt.	Av. wt.	% of body wt.
66	509.4	262.5	51.5	246.9	48.5	52.3	10.3	22.5	8.6

the beluga reserves. Investigations should continue for a more precise determination of numbers in each population. (V.A.)

Genus of Narwhals (Narwhals or Unicorns)

Genus *Monodon* Linnaeus, 1758

1758. *Monodon*. Linnaeus. Syst. Nat., ed. X, I, p. 75. *Monodon monoceros* Linnaeus, 1758.
1772. *Ceratodon*. Brünnich. Zoologiae fundamenta, p. 48. Substituted for *Monodon* Linnaeus, 1758.
1804. *Narvalus*. Lacépède. Hist. Nat. Cétacées, p. 37. *Narwalus vulgaris* Lacépède = *Monodon monoceros* Linnaeus, 1758. (V.H.)

Dimensions are the largest in the family, the body length reaching 610 cm.

Compared to the beluga, the neck is poorly developed. The head is obtuse and spherical. The mouth section is small.

The body of young animals is monochromatic, dark (bluish-gray, slaty, or slaty-blue) but in adults light-colored with numerous dark spots of irregular shape not exceeding 5 cm in diameter on the head, dorsum, and flanks. The spots on the upper parts of the head, neck, and caudal stem sometimes merge to form an overall dark background.

The skull structure in general is the same as in the genus *Delphinapterus* but asymmetry is more sharply manifest. Teeth are lacking in the lower jaw. The upper jaw has only one tooth in each half (in females, they usually do not emerge). The left tooth in males is transformed into a spiraled screwlike tusk reaching 3 m in length. The right tooth, however, is more often concealed within the gum. Sometimes two tusks grow in males. From time to time, tusks are seen among females too. Vertebrae 50 to 55; cervical vertebrae not fused. Phalangeal formula: I_{1-2} , II_{5-8} , III_{4-6} , IV_{2-4} , and V_{2-3} . Compared to the beluga, the sternum of narwhals is short and broad.

Narwhals seek food in the pelagic part of the sea. They feed mainly on cephalopods (teuthophagous) but also consume fish, possibly crustaceans as well. The periods of mating and parturition are protracted.

Narwhals are distributed in the waters of the Arctic and North Atlantic. There is no special hunting for narwhals.

The genus comprises a single species: the narwhal or unicorn, *M. monoceros* Linnaeus, 1758. (V.S.)

588

NARWHAL OR UNICORN

Monodon monoceros Linnaeus, 1758

1758. *Monodon monoceros*. Linnaeus. Syst. Nat. ed. X, I, p. 75. Northern seas of Europe and America.
1781. *Monodon narhval*. Borowski. Gemeinn. Naturgesch. d. Thierreichs, 2, p. 8.
1804. *Narwalus vulgaris*. Lacépède. Hist. Nat. Cétacées, p. 37, 142, pl. 4. Substituted for *Monodon monoceros* Linnaeus, 1758.
1811. *Ceratodon monodon*. Pallas. Zoogr. rosso-asiatica, I, p. 295. Seas of the Russian arctic ("In mare arcticum Ruthenum imperium alluente"). (V. H.)

Diagnosis

Only species of the genus.

Description

Males can attain a body length of 610 cm and females 420 cm.

A rounded small head is set off from the trunk by a weakly discernible neck (Fig. 338). The spermaceti case slightly overhanging the upper jaw gives the head its roundness. The upper lip projects slightly forward above the fleshy lower lip. The slightly convex dorsum carries a low fold of skin up to 5 cm thick and 75 cm long.

The asymmetry of the skull (Fig. 339) is manifest in the more intense development of maxillae and premaxillae on the left side while the cranium is better developed on the right side. The importance of the tusk (tooth) to the narwhal is not clearly understood. It has been suggested (Thompson, 1939) that the spiraled tusk serves to stabilize the animal body against rotation along the axis during circular movements of the caudal flukes during swimming. It is perhaps more correct to regard the tusk as a secondary sex characteristic of males (Chapskii, 1941; Sleptsov, 1955) serving as a defense organ. It is possible that the animal uses this tusk to pierce holes in the ice through which not only he himself, but also other members of the herd, i.e., females and young animals without tusks, can breathe (Tomilin, 1957).

Cervical vertebrae 7, thoracic 11-12, lumber 6-10, and caudal 26-27.

589 The main measurements of the skull (Tomilin, 1957), average of one to four animals are (in cm): condylobasal length 61; zygomatic width 39; length of rostrum 28; width of rostrum at base 21; length of lower jaw 50; and mandibular symphysis 6. (V.S.)

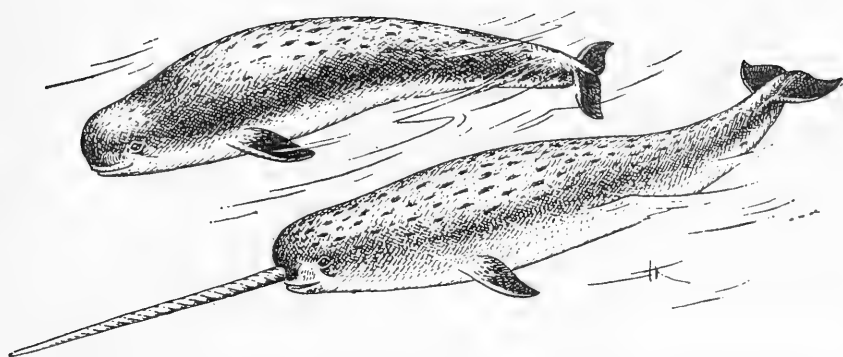
Geographic Distribution

Basin of the northern Arctic Ocean. This species lives mainly in the arctic zone, less often seen close to the coasts.¹⁹

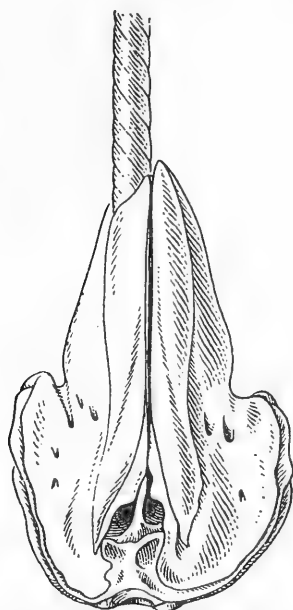
Geographic Range in the USSR

Narwhals have been observed in the Barents Sea in Novaya Zemlya at 76° N lat. (Russkaya Gavan'), in Franz Josef Land archipelago, in the midpart of the Kara Sea, around Dickson Island, and in the Chukchi Sea. In 1938, during the drifting of ice breakers "Sedov," "Sadko," and "Malygin," narwhals were sighted no less than 15 times in the region 81° 21' - 82° 15' N lat. and 136° 15' - 138° 15' E long. They were sighted

¹⁹ Distribution is equally known from the records of animal remains as from field observations.



588 Fig. 338. Narwhal, *Monodon monoceros*, male and female (figure by N.N. Kondakov).



589 Fig. 339. Skull of the narwhal, *Monodon monoceros* (figure by N.N. Kondakov).

from the floating arctic stations in June, July, and August of 1950 northwest of Wrangel Island, in 1955 north of De Long Islands, and in 1956 between Severnaya Zemlya and Franz Josef Land. Remains of narwhals have been found in the estuaries of rivers Olenek, Anabar, Khatanga, and Lena, and also on Lyakhovsk Islands, Cape Serdtse-Kamen', and in the Chukchi Sea. In the summer months narwhals are most common in the waters from 80° to 85° N lat.



589

Fig. 340. Skull of a narwhal with two tusks (figure by N.N. Kondakov).

Geographic Range outside the USSR

American Arctic, north of Labrador and Alaska and waters of Greenland (Fig. 341); known in the Canadian archipelago in Hudson Bay, Davis Strait, and in Baffin Bay right up to Smith Strait, in the waters of Spitsbergen, later in the waters of Cape Barrow and in the Beaufort Sea close to the Colville estuary. Beached narwhals or their remains have
590 been found at some points along the coasts of Greenland, in the Beaufort Sea, near Cape Gal'skett, and in Kiwalik Bay in the Chukchi Sea at 60° N lat. and 162° E long. (Tomilin, 1957, 1962; Uspenskii, 1958; Hall and Kelson, 1959; Gest, Buckley, and Manville, 1960). (V.A.)

Geographic Variation

Not established.

Biology

Population. One of the comparatively rare forms of cetaceans, this species does not form large congregations. It is more abundant in the waters of Greenland than in other parts of the range.

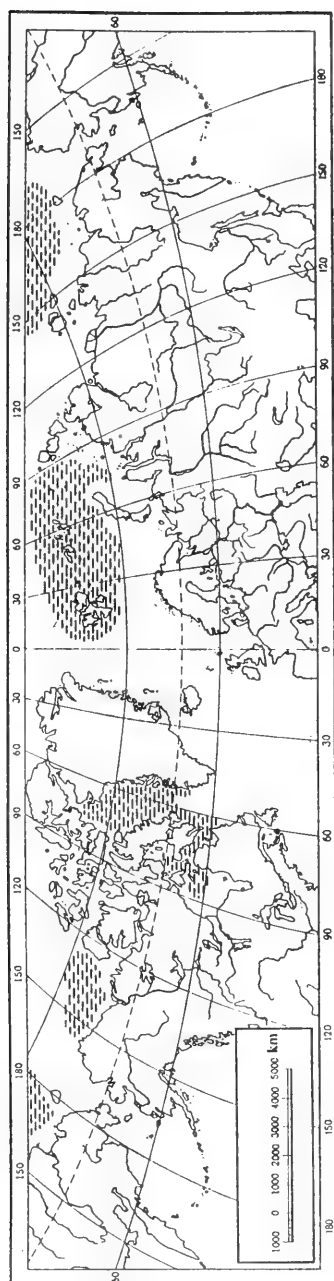


Fig. 341. Species range of the narwhal, *Monodon monoceros* (V.A. Arsen'ev).

Food. Information on this aspect is very scant. Cephalopods evidently serve as the main sustenance, followed by fish to a lesser extent. Among cephalopods, the squids *Gonatus fabricii* and possibly *Rossia*, *Bathipolypus*, *Ommatostrephes*, and some others have been detected. Fish food includes cod, flounder, halibut, skate, salmon, and herring (Smirnov, 1935; Tomilin, 1957). These animals feed predominantly in the pelagic region. The oral cavity is well adapted to feeding on cephalopods. Most of the above fish represent deep-dwelling forms.

Behavior. There are quite a number of references in the literature to narwhals being encountered in large herds numbering thousands of animals. In our times, however, such large herds have not been reported. Narwhals are most often encountered in small groups or singly; relatively large collections are very rare. Herds consisting of a relatively large number of animals are probably of mixed composition, with adult males, females, and young animals. Small herds, in some cases, consist exclusively of females with calves. Some twenty instances are known when even a relatively small herd consisted exclusively of adult males.

The narwhal usually remains far from coasts and approaches only sometimes in search of food. The animal can remain submerged under water for quite a long time, after which it surfaces eight or nine times successively at intervals of roughly 3 sec. During surfacing, the animal makes a loud expiration, flexes its body arcuately, but does not usually display the tusk above the water. Only when a group of narwhals dives in a small air hole, do their tusks project above the water (Gorbunov, 1940).

In July, 1955, in the western part of Franz Josef Land archipelago (Cambridge Bay), a group of narwhals, a hundred strong, was sighted in a state of intense excitation. Sometimes the animals flexed arcuately, leaped out of the water like dolphins or, while diving under the ice, cast their head down such that the caudal flukes rose high above the water. While emerging from under the ice they often lifted the entire anterior half of the body with the tusk above the water surface. Meanwhile, at some distance, some ten narwhals remained immobile on the surface. The diving narwhals were probably feeding. At night, the animals were quiet and stationary with tusks visible above the sea surface. Some of the tusks crossed like swords (Sushkina, 1956). Once a narwhal was seen following a ship. Instances are known of groups of narwhals abandoning the ice and remaining a long time in small air holes, thereby falling easy prey to hunters. Mixed herds of narwhals and belugas have also been recorded. Narwhals produce various sounds, such as loud gurgles, resonant groans, and howling hoots (Tomilin, 1962).

Seasonal migrations and transgressions. Observations on these aspects are very scant. In the waters of the Soviet Union, the zone of polar ice edges probably serves as the southern boundary of distribution in winter. In summer the animals ascend northward and are usually encountered beyond the 80th parallel. In Baffin Bay they arrive with the ice in Smith Strait in winter but again return south in the autumn, reaching Disko Strait by December (70° N lat.). Only some stray animals penetrate south of Sukkertoppen region (about 65° N lat.) while the main herd remains in the north. Narwhals are common from Angmagsalik village to Scoresby Sound (65 to 70° N lat.) on the east coast of Greenland in summer months (May to August) but the animals may ascend northward up to perhaps 80° N lat. or beyond.

Some distant migrations of narwhals into the south are known. Their remains have been found in Mezensk Bay of the White Sea, along the Murman coast close to the Pechora estuary, at Jan Mayen, Iceland, Faroe Islands, and along the coasts of Norway, Scotland, and England. One instance of the death of a female narwhal was recorded in the Elba estuary in Holland. In the Pacific Ocean, transgressions are known in Bering Strait and toward St. Lawrence Island. One dead narwhal was found in the region of Port Moller in the central Alaskan peninsula. In the last century, one narwhal was found on Bering Island (Commander Islands) (N. Smirnov, 1935; Tomilin, 1957; Gest, Buckley, and Manville, 1960).

Reproduction. Mating and parturition may occur at almost any time of the year (N. Smirnov, 1935). The birth of a narwhal calf was witnessed from the floating station SP-5 in the waters between Franz Josef Land and Severnaya Zemlya on July 30, 1956. It was 1.5 to 2 m long (Uspenskii, 1958). Very small as well as almost mature embryos were found at the same time (Fig. 342). The duration of gestation is not known. Usually one calf is born and twins are rare. The body length of a newborn calf hovers around 150 cm. Suckling calves are bluish-gray or slate-colored. As the

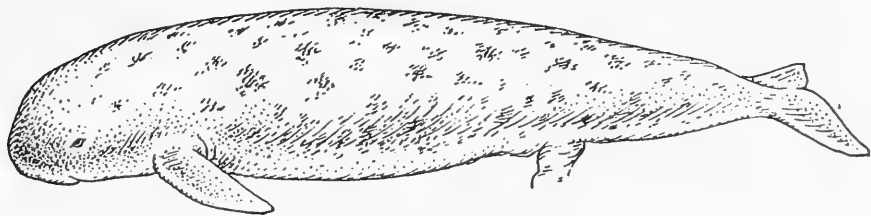


Fig. 342. Newborn narwhal (figure by N.N. Kondakov).

animal grows, the ventral part of the adult gradually lightens (white or yellowish) while the flanks and dorsum darken with innumerable random
 592 dark brown spots of irregular shape. On the dorsum, especially the upper part of the neck and head, the spots are darker and denser than on the flanks. The periods of color variation as also the degree of their consistency with the changing age of the animal have not been established (Tomilin, 1957).

Enemies, diseases, mortality, parasites, and competitors. One of the possible enemies of the narwhal is the white polar bear; the young are threatened by Greenland sharks. Only bone diseases are known in the narwhal.

Two species of lice have been found in the skin folds of the narwhal: *Cyamus monodontis* and *C. nodosus*. Among endoparasites, three species of nematodes are known. *Anisakis (Anisakis) simplex* Rudolphi, parasitizing the gullet, stomach, and intestine, has also been found in ten species of toothed whales, two species of baleen whales, and in Steller's sea lion. It has been detected in the North Sea and in the North and South Pacific Ocean. *Terranova (Terranova) decipiens* Krabbe, common in pinnipeds, seems doubtful in the narwhal. It definitely occurs in two species of baleen whales, in toothed whales, and in common porpoises. *Torynurus alatus* Leuckart is known only in the narwhal from the coast of Greenland. It has been detected in the skull cavity, eustachian tube, venous vessels, and lungs (Delamure, 1955).

Field characteristics. Spotted coloration of the dorsum and body flanks is a characteristic feature of the species. Teeth one pair but usually do not emerge among females; one tooth among males turns into a long (up to 3 m) spiraled tusk projecting forward. A dorsal fin is absent. This species inhabits predominantly the Arctic Zone and can often be seen in air holes among highly compact ice. (V.A.)

Economic Importance

Only the local Greenland people regularly catch some narwhals and utilize their products to meet personal needs. Elsewhere in the range these cetaceans are caught merely incidentally in small numbers. Hence this species has almost no economic importance.

The skin of the narwhal is quite tough and can be used for the same purposes as the skin of the beluga. The carcass of the animal is useful for preparing the same products as those from other marine mammals. The large tusk of the male can evidently be carved or sold as a souvenir because of its rarity. Narwhal tusks were highly prized at one time (Vinogradov, 1949; Tomilin, 1957). (V.A.)

SUPERFAMILY OF SPERM WHALES
Superfamily PHYSETEROIDEA Gill, 1872

Family of Sperm Whales
Family PHYSETERIDAE Gray, 1821

Dimensions range from medium to large.

The body form is diverse: the anterior half of the trunk of sperm whales is relatively short but very thick; in dwarf sperm whales, it is more elongated while the thickness is maximum between the flippers and the dorsal fin. The head may be very large, up to one-third of the body length, and obtusely flattened or slightly rounded anteriorly, or markedly smaller and more proportionate and rounded. The dorsal fin is low and humplike or quite high and falcate.

The rostrum of the skull is broadened, flattened, and has a large depression on the dorsal surface. The lower part of the spermaceti sac lies inside this depression; among males, this sac projects forward in relation to the skull bones. The occipital bone forms a high crest. The lachrymal is fused with the zygomatic. The petrosal is enlarged toward the skull. The narrow lower jaw does not extend beyond the anterior section of the head: the symphysis of both its halves usually forms not less than one-third of its length.

The teeth, located in deep alveoli, are preserved in most animals only in the lower jaw, being either rudimentary or altogether absent in the upper jaw. Keratinized projections on the palate replace the teeth functionally.

Sperm whales feed mainly on cephalopods of different sizes, including very large ones (teuthophagous).

These whales are distributed throughout the World's Ocean. The northern limit of the range extends into the Pacific Ocean from Maina-Pylgo village and Cape Navarin to the Pribilof Islands and in the Atlantic, from Davis Strait to the region west of Jan Mayen and Spitsbergen and eastward up to Kanin Nos Peninsula. The southern boundary of distribution reaches the edges of drifting ice in the Antarctic. Sperm whales are common and abundant while dwarf sperm whales are few and very rarely encountered.

Diaphorocetus Ameghino, found in the Lower Miocene, already had a skull with features characteristic of Physeteridae Linnaeus, though it was not as large as the modern forms, and had teeth in the upper jaw. Reduction of upper teeth is noticed among representatives of sperm whales from the Middle Miocene (for example, in *Aulophyseter* Kellog).

The family is usually (Simpson, 1945) divided into three subfamilies, of which one is extinct (Hoplocetinae Cabrera, six genera) and two

contemporary: Physeterinae Flower (sperm whales proper) and Kogiinae Gill (dwarf sperm whales). The total number of genera is 19. Physeterinae includes ten extinct genera and one contemporary; Kogiinae comprises one extinct and one contemporary genus. Thus the contemporary genera of the family are: sperm whales *Physeter* Linnaeus and dwarf sperm whales *Kogia* Gray. In the context of systematics, the contemporary family of sperm whales is not a complex group and its division into genera raises no doubts. However, subspecies have not been well studied.

Only one subfamily of sperm whales proper, physeterinae, with one genus of true sperm whales, *Physeter* Linnaeus, has been established for certain in the fauna of the USSR. The presence of the subfamily of dwarf sperm whales, Kogiinae, with the single genus *Kogia* Gray, has not been established but is entirely possible.

Only sperm whales are of practical importance. They are hunted in large numbers, especially in our Pacific Ocean waters. (V.S.)

594

Subfamily of Sperm Whales Subfamily Physeterinae Flower, 1864

Genus of Sperm Whales

Genus *Physeter* Linnaeus, 1758

1758. *Physeter*. Linnaeus. Syst. Nat. ed. X, I, p. 76. *Physeter catodon* Linnaeus.

1761. *Catodon*. Linnaeus. Fauna suecica, p. 18. *Catodon macrocephalus* Linnaeus = *Physeter catodon* Linnaeus. (V.H.)

Large whales with sharply manifest sexual dimorphism: males up to 18-20 m long and females up to 11-13 m.

The large head constitutes one-third of the total length of the body. The dorsal fin is weakly developed, low, and usually rounded in the form of a prominence. A few very low tubercles occur posterior to it. The broad flippers have a rounded outer margin. The caudal flukes are broad. The blowhole (nostril) is present in the anterior section of the head to the left.

The length of the rostrum constitutes more than one-half the condylobasal length of the skull. Its dorsal surface has a deep depression. The skull bones are sharply asymmetric. The right nasal bone fuses with the right premaxilla. The pterygoids are adjacent for a significant distance. Vertebrae usually 50. Teeth $\frac{0-10}{20-28}^{(19)}$.

The narrow scapula has a large coracoid process. Ribs up to 11 pairs, of which only 3 are joined to the sternum. The body color is dark and the abdomen only slightly lighter than the upper part.

The main food object is cephalopods while fishes represent an additional item. The ability to dive deep and remain long under water is a characteristic feature of sperm whales. These are polygamous animals. Various researchers have put the duration of gestation at 10 to 16.4 months. The periods of mating and parturition are protracted. Females apparently bear offspring once in two years.

These whales are distributed predominantly in the warm and temperate waters of the Pacific, Indian, and Atlantic oceans (for more details, see "Description" of the species). Females, compared to males, are more thermophilic. Significant migrations are a characteristic feature.

In USSR waters, they are encountered in the Barents Sea and in the seas of the Pacific Ocean.

Fossil remains have been found in the Upper Miocene and Pleistocene of North America and in the Lower and Middle Miocene of Europe.

These whales are of great economic importance. A large number is caught every year.

The genus comprises a single species: the sperm whale, *Physeter catodon* Linnaeus, 1758. (V.S.)

SPERM WHALE

Physeter catodon Linnaeus, 1758

- 1758. *Physeter catodon*. Linnaeus. Syst. Nat., ed. X, I, p. 76. Orkney Islands.
- 1758. *Physeter macrocephalus*. Linnaeus. Syst. Nat., ed. X, I, p. 76. "European Ocean".
- 1818. *Physeterus sulcatus*. Lacépède. Mem. Mus. Hist., Nat., Paris, 4, p. 474. Japan.
- 1822. *Physeter australasianus*. Desmoulins. Dict. class. Hist. Nat., 2, p. 618. Moluccas and New Zealand.
- 1851. *Catodon australis*. Wall. Mem. Australian Mus., I, p. 1. Australia.¹ (V.H.)

Only species of the genus.

¹ After Hershkovitz (1966); A.G. Tomilin (1957) attributes this name to MacLeay, 1851.

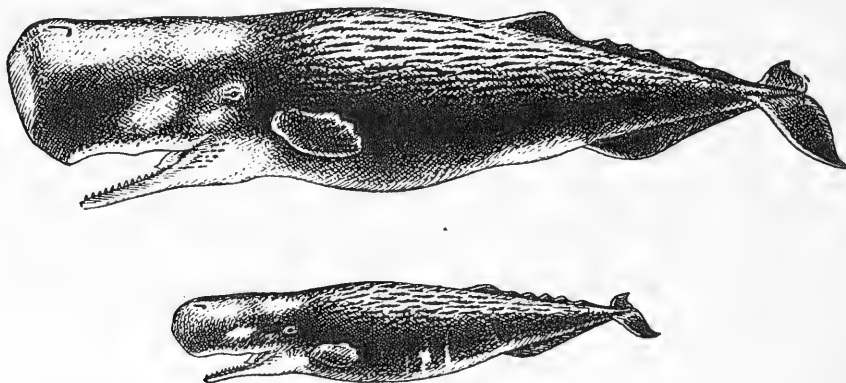
Description

The dimensions of this species are the largest of any toothed whale.²

The body is teardrop-shaped and considerably thickset in the anterior half (Fig. 343). The anterior part of the huge head terminates bluntly in a "forehead". The dimensions of the head are mainly determined by the massive spermaceti sac situated above the skull in the depressions of the maxillae and projecting beyond the anterior tip of the jaw. The spermaceti sac consists of lower [melon or "Junk"] and upper [spermatic organ or "case"] sacs made up of connective tissue with a high content of an oily liquid, i.e., spermaceti (Fig. 344). The sacs are surrounded by connective tissue and muscles. Liquid wax (cetin) is the main constituent of spermaceti (96.99%). Adult sperm whales carry 1.0 to 5.7 tons of spermaceti.

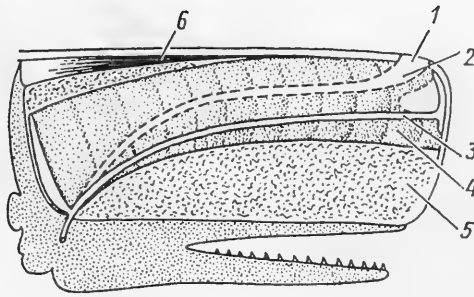
The head of males is relatively larger (up to one-third of body length) than in females (slightly more than one-fourth body length). With age, the head section of the sperm whale is relatively enlarged while the caudal end is correspondingly shortened (Ivanova, 1955). The relative increase in head size commences even in the fetal growth period (Ivanova, 1959).

The cross section of the head appears rounded from above and keel-shaped from below (anterior to the jaw). The narrow lower jaw with the mouth closed is held to the head by the connective tissue edges [lips] of the upper jaw. The unpaired blowhole is S-shaped and located, unlike
596 in other cetaceans, in the anterior part of the head left of midline and is



595 Fig. 343. Sperm whale, *Physeter catodon*, male and female (figure by N.N. Kondakov).

² Data on the weight of the animals and of the various parts of their body are given later under "Economic Importance" and Table 62 (p. 838).



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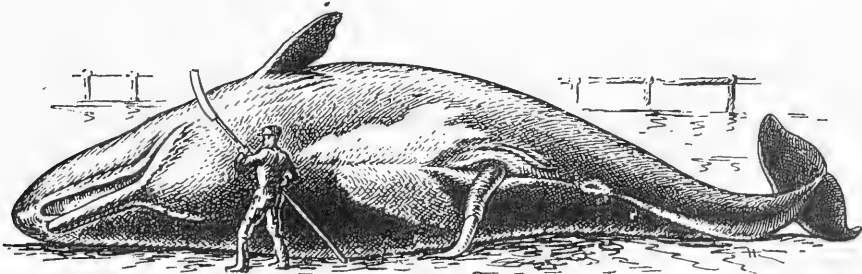
Fig. 344. Section of the head of the sperm whale, *Physeter catodon* (figure by N.N. Kondakov): 1—blowhole; 2—left nostril; 3—right nostril; 4—upper spermaceti sac [spermaceti organ or “case”]; 5—lower spermaceti sac [“melon” or “Junk”]; 6—sinew-tendon layer.

20 to 60 cm long. The eyes are roughly at the center of the head at the level of the posterior corners of the mouth. The section of the orbital aperture is 6–12 cm long and the diameter of the orb 15–17 cm. Small (up to 1 cm long) crescent-shaped ear openings are located posterior to the eyes and slightly below them.

The head is set off from the trunk by a faintly perceptible neck. The trunk attains maximum thickness in the zone of the flippers but thins out gradually thereafter. The flippers are short and broad, with rounded outer edges. The large lobes of the caudal flukes are separated by a deep notch. Two to six very low tubercles are located posterior to the humplike dorsal fin. A rather low leathery keel runs along the lower side of the caudal stem.

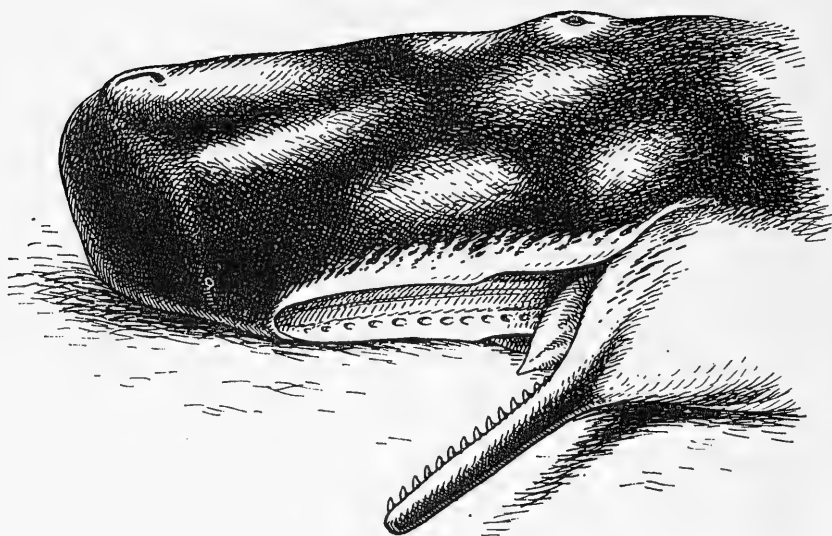
The integument of the sperm whale is quite thick (Table 58).

In some sperm whales the thickness of the abdominal skin [epidermis plus dermis] may go up to 50 cm. The thickest epidermis and the densest



596

Fig. 345. Sperm whale, *Physeter catodon* (ventral view) (figure by N.N. Kondakov).



596 Fig. 346. Head of a male sperm whale, *Physeter catodon* (figure by N.N. Kondakov).

597 Table 58. Skin [epidermis plus dermis] thickness in different sections of the trunk of the sperm whale (in cm) (V.E. Sokolov)

Sex	Date of birth	length, m	Abdomen			Dorsum		Body flanks around flippers	Lateral part of head
			Under flippers	Around navel	Before vulva	Above flippers	Anterior to dorsal fin		
Female	Aug. 7	10.2	15	10	—	21	—	6.5	6
Female	Aug. 7	9.8	18	14.3	22	20	25	9.5	8.5
Female	Aug. 7	9.3	16	11.5	15.5	12	16	10	7.5
Male	Sept. 13	14.8	31	30	—	38	33	22	8

collagen fiber fascicles in the dermal layer occur on the anterior surface of the head. This is explained not only by the fact that this part of the head faces maximum resistance against water while swimming, but also by the fact that males in the period of mating butt each other with their “foreheads” just as rutting rams do (Sleptsov, 1955). The epidermis of the sperm whale is characterized by prominent projections of epidermal barriers extending into the dermal papillae. These projections, in many cases, have thickened distal and thin proximal sections. On the dorsum and flanks the skin surface is corrugated. In the depressions between the

597 tubercles, the epidermis forms projections into the dermal layer. On the throat 10 to 40 longitudinal furrows occur, up to 1 cm in depth and 5 to 50 cm in length (Tomilin, 1957). It is probably because of these that the throat can expand slightly while swallowing a large quarry (Beddard, 1900).

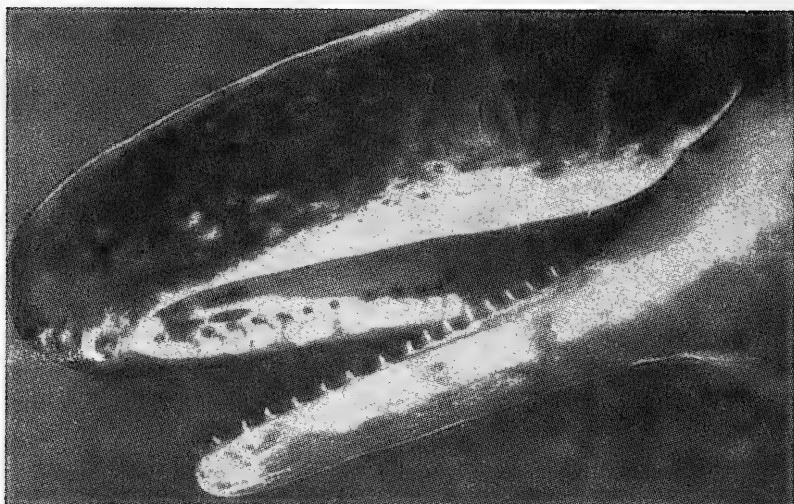
A typical leathery callosity on the dorsal fin is regarded as a secondary sex-related feature of females (Kasuya and Ohsumi, 1966).

The body color is monochromatic dark (black, blackish-brown, blackish-cinnamon) with a much lighter-colored abdomen bearing an irregular white patch. The outline of this patch varies sharply in different animals. The sperm whales encountered in the waters of Japan can be classified into four color groups (Omura, 1950b): (1) with continuous dark gray color all over the body; (2) with a slightly lighter coloration on the lower side of the head and the lower jaw; [(3) with a light coloration on the lower side of the head and the lower jaw—this is an addition to Omura's classification]; (3) with a light coloration all over the head; and (4) with a very light coloration all over the trunk. Animals of the third group are the rarest. Sperm whales caught off the Kuril Islands are mainly of two colors, dark and light, and form no less than eight variations of the
598 white pattern (Ivanova, 1959*). With age, the color of the animals turns somewhat lighter. Many white and gray patches, bands, scratches, etc., formed as a result of skin infections caused by ectoparasites, lampreys, and suckers and hooks [jaws resembling the parrot's beak] of squids are seen on the skin surface. Such patches are more among females than males (Omura, 1950b).

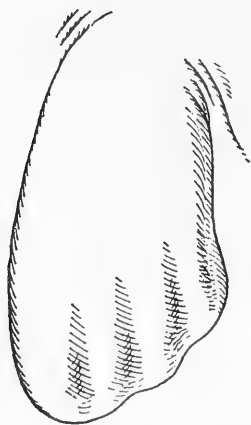
In the sharply asymmetric skull the upper lateral sections of the maxillae form crests laterally surrounding the base of the spermaceti sac. The horizontally disposed palatines are covered from the rear by the pterygoids. The halves of the lower jaw form a symphysis constituting up to 50% (or slightly more) of the entire jaw length (Fig. 349). The relative length of the rostrum and mandibular symphysis increases with age (Tomilin, 1957).

Cervical vertebrae 7, thoracic 11, lumbar 8, and caudal 24. Information on the fusion of the cervical vertebrae is contradictory. Some scientists assume that the cervical vertebrae of the sperm whale fuse into two independent groups of 1 to 3 and 4 to 7 vertebrae (Sleptsov, 1955). According to other authors, the sperm whale represents a unique case among cetaceans with its atlas remaining free while all the other vertebrae are fused (Tomilin, 1957). The level of the transverse processes of the lumbar vertebrae is much lower than that of the thoracic.

In the five-digit limb (Fig. 348) the humerus is sometimes fused with the ulna and the radius. Phalangeal formula: I_1 , II_5 , III_5 , IV_4 , and V_3 (Beddard, 1900).

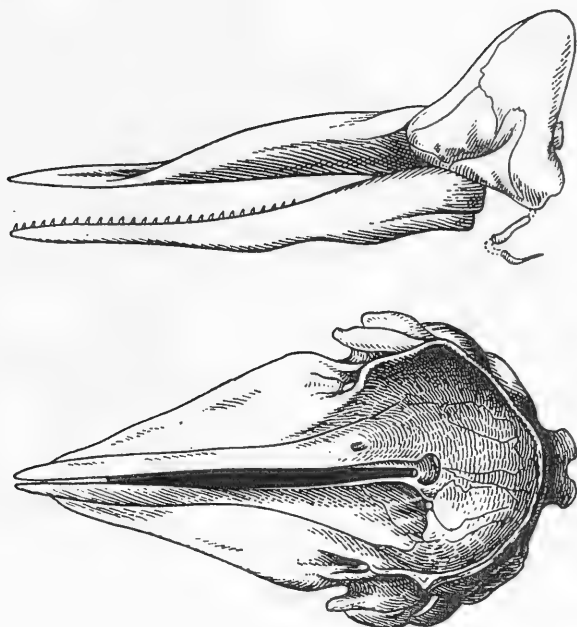


597 Fig. 347. Head of a female sperm whale, Kuril Island, 1962 (photograph by A.V. Yablokov).



598 Fig. 348. Flipper of the sperm whale, *Physeter catodon* (figure by N.N. Kondakov).

The peg-shaped homodont teeth of the sperm whale, often slightly curved midlength, can reach large proportions, up to 27 cm in length (Yablokov, 1958a), with the largest occurring in the middle of the jaw. The teeth are larger among males than females. Large teeth are encountered only in the lower jaw. The teeth on the upper jaw are small, not strong, or may be altogether absent. The number of upper teeth among



599 Fig. 349. Skull of the sperm whale, *Physeter catodon* (figure by N.N. Kondakov).

males varies from nil to 19 and among females from nil to 10 (Sleptsov, 1955). The tooth crowns in embryos may have three cusps (Nishiwaki, Hibiya, and Ohsumi, 1958). The teeth of calves usually emerge by the end of the lactation period. With advancing age, the size of the teeth increases considerably.³ Mandibular teeth begin to wear out a few years after birth (the anterior and middle ones in the first instance), sometimes right up to the base, although the upper and lower teeth may not come into contact with each other. The gaps between the teeth vary from 3.5 to 15 cm. The teeth are firmly set in the alveoli and rise above the gum level only to one-sixth to one-fifth of their length; intense growth of cement is a characteristic feature. The volume of the pulp cavity can measure up to one-half that of the tooth. The teeth of adult animals have no enamel layer (Yablokov, 1958a).

The total length of the largest male caught was 20.7 m, of the female 15.8 m. The average length of 2,510 males caught in the Northern hemisphere was 14.6 m and of 15,526 males caught in the Southern hemisphere 15.9 m; the average length of 1,190 females (waters of Japan) was 10.64 m (Tomilin, 1957).

³ A method was suggested for determining the age of sperm whales by counting the number of layers in a longitudinal slice of tooth (Nishiwaki, Hibiya, and Ohsumi, 1958).

The average main body measurements as percentage of body length among males and females caught off the Kuril Islands (Tomilin, 1957) are: distance from tip of snout to blowhole in males 2.30 (two measurements) and females 1.50 (2); distance from anal opening to notch ¹⁵⁹⁹ between caudal flukes 30.30 (94) and 32.20 (46); height of dorsal fin 2.40 (147) and 2.60 (58); length of dorsal fin 8.00 (145) and 8.10 (62); length of flippers 9.6 (147) and 9.7 (74); maximum width of flippers 4.90 (26) and 4.90 (20); anterior-to-posterior width of caudal flukes 9.40 (192) and 9.70 (88).

The main skull measurements (see Fig. 349) of three male sperm whales (Tomilin, 1957; Omura *et al.*, 1962) are (in cm): condylobasal length 510, 450 and 360; interorbital width 220, 170; length of rostrum 370, 320, and 250; width of rostrum at base 150, 170, and 120; and length of lower jaw 450, 300 [The authors gave the skull measurements in decimeters instead of centimeters. I have added a zero to them to convert them to centimeters—Ed.] (V.S.)

Geographic Distribution

Sperm whales inhabit the warm and temperate zones of the World Ocean and are encountered almost everywhere. The summer ranges of males and females are diverse: the former are encountered at very high latitudes, reaching the arctic zone in the Southern hemisphere; the latter do not emerge beyond the temperate waters throughout the year.

Geographic Range in the USSR

Constitutes a small section of the total range of the species. These animals are encountered in the basin of the Atlantic Ocean in the southern part of the Barents Sea: along the Murman coast, possibly up to Kanin Peninsula in the east (Fig. 350). In the Pacific Ocean they are distributed in the Sea of Japan where they are sometimes sighted in Peter the Great Gulf and even transgress into Zolotoi Rog Bay. They are encountered in the waters of the Kuril Islands, predominantly from the Pacific Ocean side. Large males inhabit the Sea of Okhotsk, mainly its northeastern section. Farther northward, these animals are known in Kronitskiy and Kamchatka gulfs off the southeastern coast of Kamchatka and around the Commander Islands. They have been sighted off Cape Navarin in the southern part of the Gulf of Anadyr.

Geographic Range outside the USSR

Distributed almost everywhere in the North Atlantic Ocean (Fig. 351). Throughout the year, sperm whales are sighted off the Cape Verde,

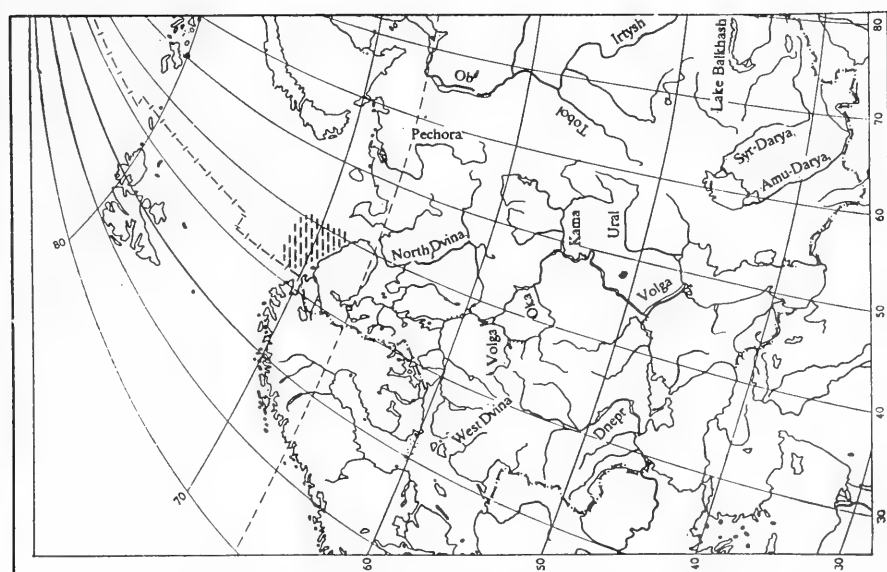
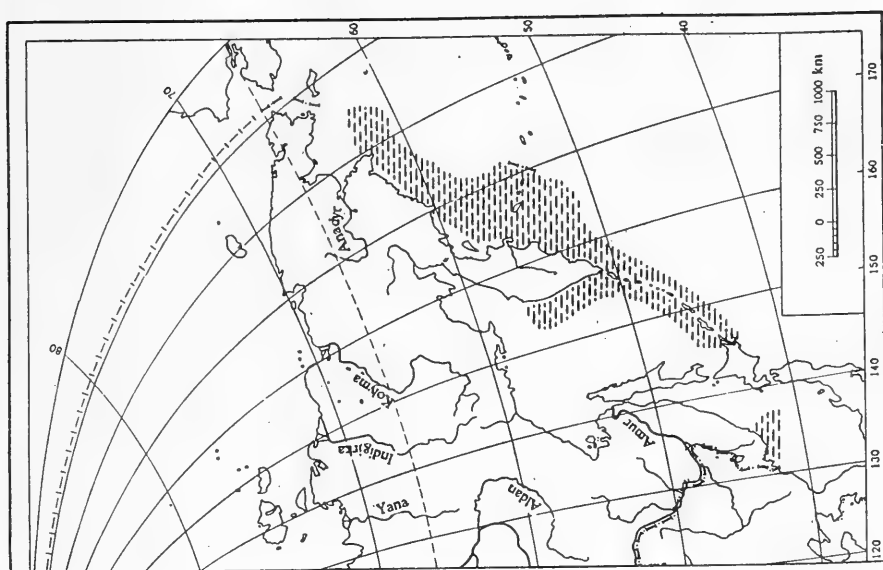


Fig. 350. Range of the sperm whale, *Physeter catodon*, in the USSR (V.A. Arsen'ev).

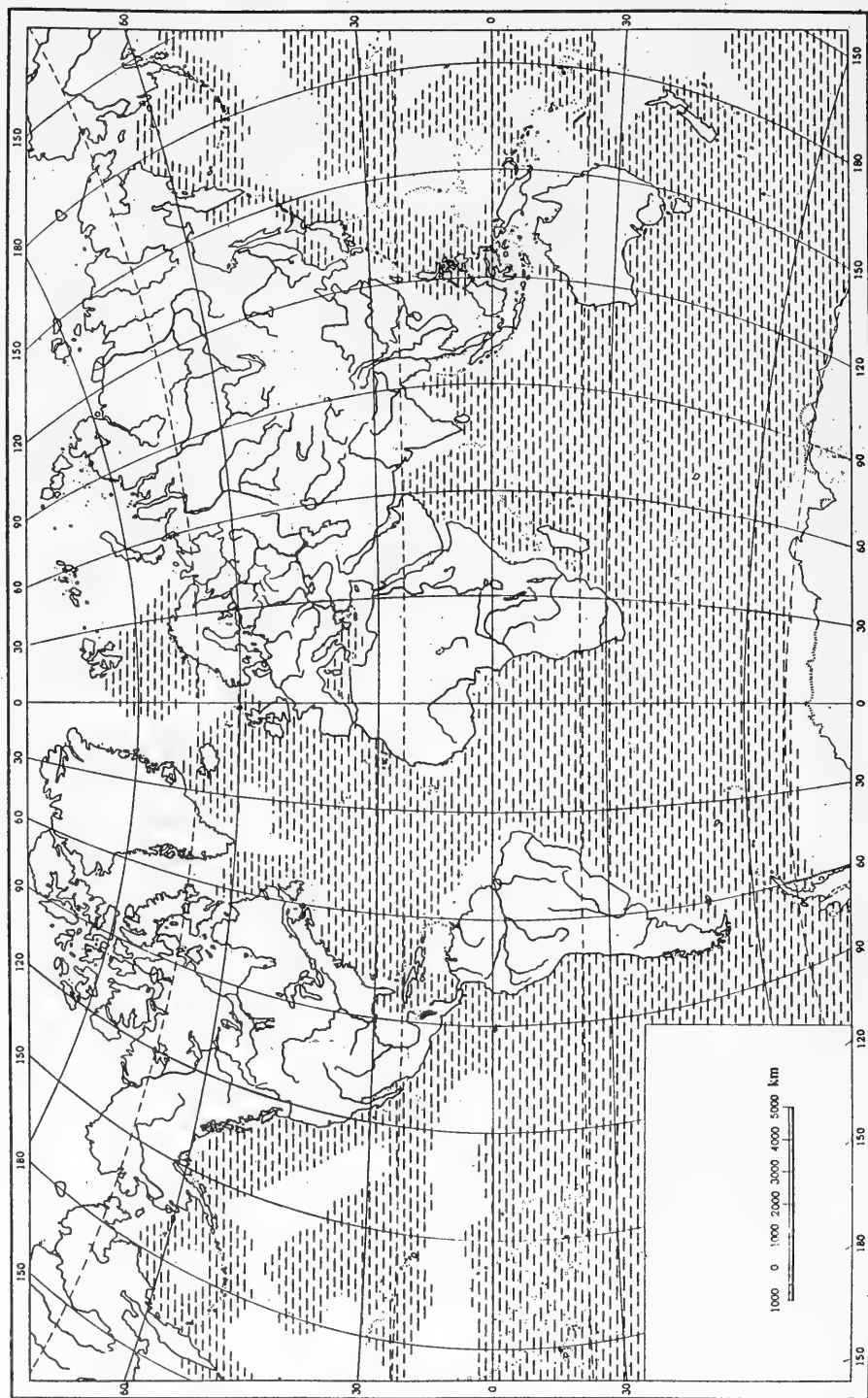


Fig. 351. Species range of the sperm whale, *Physeter catodon* (V.A. Arsen'ev).

Canary, Azores, and Madeira islands and along the coasts of Spain and Portugal, off the Antilles and Bermuda islands, and along the coasts of Florida, i.e., up to 520 - 15° N lat. They are quite common in the Mediterranean Sea. They are not infrequent in the waters of Great Britain, off the Orkney and Shetland islands, widely distributed along the coasts of Norway, in the waters of Iceland, and off the Faroe Islands. Data on their distribution along the American mainland between Florida and Newfoundland are altogether lacking although some random observations suggest that these animals are encountered here. In the North Atlantic, sperm whales reach Newfoundland, Labrador, Davis Strait, and the coasts of southern Greenland. They inhabit the waters of Jan Mayen (70° N lat.) and even Spitsbergen (around 80° N lat.).

602 Information on the distribution of sperm whales in the equatorial section of the Pacific Ocean is highly approximate. They have been assumed to be quite common close to Kalimantan, Celebes, Mariana, Marshall, and Bonin islands, and are possibly encountered in the Sulu and Banda seas, i.e., not only reach the equator, but sometimes even the equatorial waters of the Southern hemisphere. The contemporary regions of wintering of northern sperm whales are possibly bounded by the line: Bonin Islands-Hawaii-California coast (Berzin and Rovnin, 1966), i.e., within 15 to 20° N lat. Sperm whales are common along the southern and eastern coasts of Japan but rare in the East China Sea and in the southern part of the Sea of Japan. In the northeastern half of the Pacific Ocean, sperm whales are distributed from California to the Gulf of Alaska and the Alaskan Peninsula and along the islands of the Aleutian range. In the Bering Sea, they are common in Bristol Bay and in the waters of the Pribilof Islands, occupy the eastern part of the sea bound by the shallow-water line running from Bristol Bay to Cape Navarin on the Asian coast and probably up to St. Lawrence Island.

In the Southern hemisphere, sperm whales occupy the entire zone of tropical and temperate waters. In the Atlantic Ocean, they are known from the coasts of Brazil to the Falkland Islands and Tierra del Fuego in the south, and sighted in the waters around Tristan da Cunha, Ascension, and St. Helena islands. In the eastern part of the Atlantic, they are common from the equatorial waters of the Gulf of Guinea to the southern tip of Africa. In the Indian Ocean, the largest number probably inhabits the waters of southeastern Africa and Madagascar; they are known off the Mascarene, Seychelles, Cocos, and Christmas islands, and along the coasts of Australia. Penetrating northward, the distribution crosses the equatorial zone and this animal is known in the Arabian Sea and transgresses into the Red Sea. In the southern half of the Pacific Ocean,

sperm whales are abundant along the coasts of Peru and common in the waters of Chile. They are encountered close to numerous islands, including Fiji, Samoa, etc., and are common in the waters of Australia and New Zealand. In the summer months male sperm whales are widely distributed in the Antarctic waters and reach the southern Arctic zone (Kirpichnikov, 1950b; Tomilin, 1957; Berzin and Rovnin, 1966; Berzin, 1971).

In spite of the fact that the two ranges of the species—northern and southern—are distinct, there is no real demarcation in the distribution of sperm whales. They are encountered in the equatorial zone of the Northern and Southern hemispheres throughout the year and hence it is very difficult to draw the boundary of distribution in either hemisphere. While a demarcation is possible in the Atlantic Ocean (though highly approximate), it is difficult to do so in the Pacific Ocean. Apparently the equatorial zone serves as the area of contact between the northern and southern populations of the sperm whale but information is not sufficient to resolve this problem. (V.A.)

Geographic Variation

A comparative morphological study of sperm whales from different parts of the World Ocean revealed no significant differences in the body proportions (Ivanova, 1955, 1961). However, some difference in the overall dimensions does exist between the northern and southern sperm whale populations (Nishiwaki, 1955). Based on this and the time differential in the main biological rhythms of the whales of the Northern and Southern hemispheres, two subspecies of sperm whales are recognized (Tomilin, 1957). Only one of these subspecies is found in the USSR.

Northern sperm whale, *P. c. catodon* Linnaeus, 1758 (syn. *macrocephalus*).

Animals of relatively smaller dimensions, with the males measuring an overall length of 14.6 m (North Pacific Ocean).

They are encountered in the Barents, Japan, Okhotsk, and Bering seas, and the Pacific Ocean.

Outside the USSR, they are found in the North Pacific and Atlantic oceans.

- 603 Systematic relationships between the sperm whales of the North Pacific and Atlantic oceans have not been studied. Evidently these populations are highly isolated (amphiboreal distribution) and possibly may not be identical. The name *sulcatus* Lacépède could be applied to the Pacific population.

Outside the USSR, some scientists recognize the form *P. c. australasianus* Demoulins, 1827,⁴ characterized by very large dimensions (average length of males 15.9 m).

These animals are encountered in the warm and temperate waters of the Atlantic and Pacific oceans in the Southern hemisphere, the Indian Ocean, and the Antarctic.

The interrelations between the two subspecies of sperm whales in the equatorial zone, especially in the Pacific Ocean, have not been studied. It is possible that many local herds of sperm whales exist in different parts of the species range; sometimes such herds can be localized in a relatively small water body (Klumov, 1955) (see "Seasonal Migrations and Transgressions"). (V.A. and V.H.)

Biology

Population. The sperm whale can be regarded as one of the more abundant species of large whales. The population is perhaps most abundant in the Pacific Ocean. The probable population of the sperm whale in the North Pacific Ocean has been put at roughly 150,000 (Nishiwaki, 1966). Up to 4,000-5,000 sperm whales were caught in some years off the coasts of Chile and Peru, indicating a large population of these whales in the South Pacific Ocean; they are also abundant in the other waters of the Southern hemisphere. Thus, in some years in the Antarctic alone, up to 6,000-7,000 male sperm whales were caught. Insofar as the North Atlantic is concerned, even approximate population data are not available. It is probable that the population here is relatively small, which is supported by the comparatively low level of hunting. The maximum number of sperm whales is caught in the waters of the Azores where the total catch sometimes does not exceed 1,000 per year.

Food. Two groups of animals, cephalopods and fish, constitute the main food of sperm whales in both the Northern and Southern hemispheres, with cephalopods predominating. The food of sperm whales has been studied in great detail in the North Pacific Ocean. Data for the other regions of the World Ocean are fragmentary and incomplete (Table 59).

Three species of squids predominate in the food of the sperm whale from the Bering Sea: *Gonatopsis borealis*, *Gonatus magister*, and *Moroteuthis robusta*; *Meleagroteuthis separata* is of lesser importance (Table 59). Among the fishes, redfish occupies first position of importance as a food item. It is followed by the smooth lumpsucker

⁴ A.G. Tomilin (1957) designated this form as *P. c. australis* MacLeay, 1851, which is hardly correct (see synonyms and note on p. 801).

Table 59.

Bering Sea (Berzin, 1959)	British Columbia (Pike, 1950b)	Kuril Islands (Betesheva and Akimushkin, 1955; Akimushkin, 1957; Betesheva, 1960, 1961; Tarasevich, 1963)
Cephalopods	Cephalopods	Cephalopods
<i>Gonotopsis borealis</i>	<i>Gonatus fabricii</i>	<i>Gonatus magister</i>
<i>Gonatus magister</i>	<i>Moroteuthis robusta</i>	<i>Gonatus fabricii</i>
<i>Gonatus fabricii</i>		<i>Taonius pavo</i>
<i>Moroteuthis robusta</i>	Fish	<i>Moroteuthis robusta</i>
<i>Meleagroteuthis separata</i>		<i>Onychoteuthis banksii</i>
<i>Galliteuthis armata</i>	Sea perch:	<i>Architeuthis japonica</i>
<i>Onychoteuthis banksii</i>	<i>Sebastes ruberrinus</i>	<i>Meleagroteuthis separata</i>
<i>Chroteuthis veranyi</i>	<i>Sebastes</i> sp.	<i>Chroteuthis veranyi</i>
	Ragfish, <i>Icosteus aenigmaticus</i>	<i>Galliteuthis armata</i>
Fish	Skate, <i>Raja rbina</i>	<i>Stigmatoteuthis dofleini</i>
	Arctic lamprey, <i>Lampetra japonica</i>	<i>Octopodoteuthis longiptera</i>
Smooth lumpsucker,		<i>Cystoloteuthis berhingiana</i>
<i>Aptocyclus ventricosus</i>	Salmon, Salmonidae	<i>Paroctopus conispadiceus</i>
Perches, <i>Sebastes</i>		<i>Japattella heathi</i>
(few species)		<i>Grimpoteuthis albatrossi</i>
Rat-tails, <i>Coryphaenoides</i> sp.		<i>Alloposus mollis</i>
Lancetfish, <i>Alepisaurus aesculapius</i>		<i>Octopus gilbertia</i>
Skates, <i>Raja</i> (two sp.)		<i>Cirroteuthis</i> sp.
Pacific lamprey, <i>Entosphenus tridentatus</i>		<i>Amphitreus</i> sp.
Sculpins, <i>Myoxocephalus</i> sp.		<i>Octopus</i> sp.
		Octopodidae sp.
		Fish
		Black rat-tail:
		<i>Coryphaenoides acrolepis</i>
		Albatross rat-tail, <i>C. pectoralis</i>
		Piked dogfish, <i>Squalus acanthias</i>
		Lancetfish, <i>Alepisaurus aesculapius</i>
		Pacific saury, <i>Cololabis saira</i>
		Pacific cod, <i>Gadus morhua macrocephalus</i>
		Alaska pollock, <i>Theragra chalcogramma</i>
		Smooth lumpsucker, <i>Aptocyclus ventricosus</i>
		Humpback salmon, <i>Oncorhynchus gorbuscha</i>
		Navaga, <i>Eleginus navaga gracilis</i>
		Podonema, <i>Podonema longipes</i>
		Sharks, <i>Somniosus</i> sp.
		Anglerfish, <i>Oneirodes</i> sp.
		Sculpins, Cottidae gen. sp.
		Salmon, <i>Oncorhynchus</i> sp.
		Greenlings, <i>Pleurogrammus</i> sp.
		Skates, <i>Raja</i> sp.

Food objects of sperm whales

Japan (Mizue, 1951b) Azores Islands (Clarke, 1956) Antarctic (Korabel'nikov, 1959)

Cephalopods	Cephalopods	Cephalopods
Squids	<i>Histioteuthis bonnelliana</i>	<i>Onychoteuthis banksii</i>
	<i>Cucoteuthis unguiculatus</i>	<i>Architeuthis</i> sp.
Fish	<i>Tetronychoteuthis dussumierii</i>	Squid (genus not identified)
	<i>Lepidoteuthis physeteris</i>	
Pacific cod, <i>Gadus macrocephalus</i>	<i>Ancistrocheirus lesneuri</i>	Fish
		Anglerfish, <i>Ceratias holböllii</i>
Alaska pollock, <i>Theragra chalcogramma</i>	<i>Loligo forbesi</i>	
	<i>Architeuthis</i> sp.	Patagonian toothfish, <i>Dissostichus eleginoides</i>
Scorpionfishes:		Southern putassu, <i>Micromesistius australis</i>
<i>Sebastes flammeus</i>	Fish	
<i>Sebastes iracundus</i>		
	Long-finned tuna (albacore), <i>Thunnus alalunga</i>	Skate, <i>Raja griseocaudata</i>
Pacific saury, <i>Cololabis saira</i>		
Pacific sardine, <i>Sardinella melanosticta</i>	Anglerfish, <i>Ceratias holböllii</i>	
	Atlantic footballfish, <i>Himantolophus greenlandicus</i>	
Round herring, <i>Etrumeus micropus</i>		
Japanese anchovy, <i>Engraulis japonica</i>	Barracuda, <i>Sphyræna</i> sp.	
Pacific mackerel, <i>Pneumatophorus japonicus</i>		
Spotted mackerel, <i>Scomber tapeinocephalus</i>		
Sharks, Selachii		

which, however, is encountered in the stomach of sperm whales more often than any other fish. The ratio of the various groups of animals in the food of the sperm whale is as follows: of the 107 stomachs with food, 69 (64.4%) contained only squids, 28 (26.2%) squids and fish, and 10 (9.4%) only fish. The importance of cephalopods and fish in the food of sperm whales undergoes variation relative to the region of habitation.

In the waters of the Commander Islands, 74.4% of the stomachs analysed contained squids exclusively, 23.9% squids together with fish, and only 1.4% fish exclusively; for the region of the western islands of the Aleutian range, these values were respectively: 54.0, 26.9, and 19.1%, and in Olyutorskiy Gulf and adjoining waters 35.7, 35.7, and 28.6% (Berzin, 1959).

604 The stomach of sperm whales from the waters of the Kuril Islands (360 stomachs) contained 28 varieties of cephalopods (21 squids and 7 octopuses). Cephalopods constitute about 95% (by weight) of the food intake of the sperm whale and fish less than 5%, although the latter were detected in almost one-third of the sperm whales investigated. Squids are of basic importance among cephalopods; octopuses constitute no more than 4% of the intake. But only seven species of squids are of practical importance as food: *Gonatus magister*, *G. fabricii*, *G. simile*, *Taonius pavo*, *Galliteuthis armata*, *Chiroteuthis veranyi*, and *Maleagroteuthis separata* constitute up to 80% of the cephalopods consumed, with 60% accounted for by the three species of the Gonatidae family alone. Cuttlefish, abundant in the Far Eastern seas, have not been found in the stomach of the sperm whale (Betesheva and Akimushkin, 1955; Akimushkin, 1957; Betesheva, 1960, 1961).

606 In the waters of Japan an analysis of 1,627 stomachs showed that squids represent the main food here too, although octopuses were found quite often but in small quantities. All the other food objects were comparatively rare. The male sperm whale feeds on a more diverse diet than the female (Mizue, 1951). The species of cephalopods were not indicated in this report.

In the waters of British Columbia, where only 50 stomachs were investigated, squids were similarly found to be of primary importance.

Frequency of Encounter (Number of Stomachs) of
Various Objects in the Food of Sperm Whales from
the Waters of British Columbia (Pike, 1950b)

Squids	35
Ragfishes (Icosteidae)	16
Sea perch	16
Skates	9
Salmon (?)	3
Lamprey	1

Squids serve as the main food of Antarctic sperm whales too: fish was found in only 6 (5.2%) of the 129 stomachs investigated (Korabel'nikov, 1959). According to the latest data, the large Antarctic toothfish is often found in the stomach of sperm whales from various regions of the Antarctic (V.L. Yukhov).

Cephalopods have been recorded as the main food of sperm whales from many other regions of the World Ocean: the North Atlantic, the Mediterranean Sea, tropical zone, and along the coasts of Australia (Tomilin, 1957) (see Table 59).

Sperm whales consume mainly comparatively small squids, 30-40 to 100 cm and less often 150 cm long, but sometimes the stomachs have contained giant animals. Thus a sperm whale 14.3 m long killed in the Azores in 1955, contained a mollusk (with tentacles) 1,049 cm long, weighing 184 kg (Clarke, 1956) (Table 60).

In the Azores the main food of males as well as females consists of comparatively small squids of nearly identical size even though the male is considerably larger than the female. Sponges, crabs, crustaceans, and even bits of the skin of pinnipeds, sometimes found in the stomach of sperm whales, are merely items swallowed incidentally.

Stomachs with a large volume of food are relatively rarely seen. Of the 264 stomachs (Kuril Islands) analyzed, 13 (4.9%) were well filled, 28 (10.6%) were moderately full, 125 (47.4%) contained little food, and 98 (37.1%) were empty (Tarasevich, 1963). The weight of the stomach contents of 120 sperm whales showed 33% with 4 to 10 kg of food, in some cases going up to 200 [sic] kg (Betesheva and Akimushkin, 1955). Most often, the stomachs revealed only the "beaks" of squids, sometimes

606 Table 60. Sizes of squids consumed by sperm whales (Clarke, 1956)

Mantle length of squids, cm	Squids found			
	Male sperm whales		Female sperm whales	
	Number	%	Number	%
60-90	41	59	28	67
90-150	26	37	13	31
150-180	2	3	—	—
180-240	1	1	1	2
Total	70	100	42	100
Average length of squids, cm	95		92	

more than 10,000. The maximum number of beaks found was 28,000, corresponding to the consumption of 14,000 squids. This, however, does not represent a one-time intake since beaks are digested very slowly (or not at all) and probably accumulate over a rather long period.

It is interesting that the squid *Ommatostrephes sloanei-pacificus*, inhabiting the upper horizons of the sea and most abundant in the Far Eastern waters, is of almost no importance in the food of the sperm whale and that the abundant cuttlefish, living close to the surface, is not touched at all. The main food consists of bathypelagic species of cephalopods and fish, most of which do not rise to a depth of less than 500 m and some of which live at depths of 1,000 m or less (Akimushkin, 1954b). Thus, sperm whales catch their quarry at depths of not less than 300 to 400 m, where these whales have almost no food competitors with the possible exception of beaked whales (Ziphiidae). In search of food, sperm whales can descend right to the ocean floor since their stomachs sometimes contained bottom-dwelling deepwater animals.

In the 1960s, with the increasing geographic spread of sperm whale hunting, more information has become available about the food of these whales in regions earlier not studied. In the open waters of the northeastern part of the Pacific Ocean, the predominant contents of the stomach of sperm whales were the remains of squids, mainly *Taonius pavo*, *Chroteuthis veranyi*, *Meleagroteuthis separata*, *Galiteuthis armata*, and *Gonatus magister*. Among fish, the following were encountered: *Alepisaurus aeusculapius*, *Pseudopentaceros richardsoni*, *Sebastes alutus*, and *Aptocyclus ventricosus*. The stomach of sperm whales from the waters of central California revealed the squids *Moroteuthis robusta* and *Gonatus borealis*, and among fish, the sharks *Apristurus brunneus* and *Squatina californica*, and sablefish, greenling, and lanternfish (Tarasevich, 1968; Berzin, 1971). In the waters of New Zealand and the nearby islands, squids were found in 84% of the stomachs studied. Remains of scorpionfish, skates, sharks, some invertebrates (fire salpians, shrimps) and even brown algae were detected. In the southern part of the Indian Ocean the stomach of sperm whales predominantly contained squids, including large ones (up to 9 m [sic] in length). Barracuda and sometimes porcupinefish were among the fishes frequently encountered in the stomach contents.

On the whole, the main food of the sperm whale every where is cephalopods (squids up to 80% of intake and octopuses), including roughly 40 species and constituting not less than 95% of the total weight of the food intake. The stomach of sperm whales also contained the remnants of over 50 species of fish but, in spite of this diversity, fish account for no more than 5% of the total intake. Most of the animals serving as food objects of the sperm whale are deepwater species (Berzin, 1971).

In the regions of summer habitation, depending on age and size of animals, male sperm whales generally form groups of definite composition. The groups most often consist of comparatively same-sized animals rather than animals of different sizes. Of the 23 groups analyzed in the Gulf of Alaska, 18 (78.3%) consisted of whales of nearly similar size and only five (21.7%) of animals of different sizes. It has been suggested that the reason for animals of the same size grouping together lies in their identical abilities for getting at food available at different depths. Large whales can dive deeper and feed at places where much smaller animals cannot. The same-sized groups of very small whales usually consist of nearly same-aged animals (with a difference of one or two years). In groups consisting of much larger whales, the age differences of the members are greater (sometimes 10 years). This factor probably determines the high individual variations in the dimensions of adult whales whose growth has ceased (Tarasevich, 1967a).

The nature of diving of the sperm whale is typical they can remain submerged under water for up to an hour and sometimes even longer (two hours is considered maximum). Before prolonged submergence, the sperm whale dives sharply, its body is steeply curved or humped and the bent caudal stem is visible on the sea surface. The animal dives almost vertically and, in most cases, the caudal flukes are displayed above the water. The appearance of this "butterfly form" above the sea surface serves as a positive indication that the whale has submerged for a long time and may surface very far from the site of submergence.

The maximum depth of submergence of the sperm whale has not been established. Nineteen instances are known of damage to underwater cables caused by sperm whales entangled in them, exclusively in tropical and temperate waters (between 46° S lat. and 46° N lat.). The depth at which dead sperm whales were detected ranged from 118 to 1,116 m. Having become entangled in the cable, the sperm whale grips it with the teeth, tears the insulation, and thereby damages it. In 1951, a cable
609 connecting Lisbon and Malaga revealed this type of damage at a depth of 2,200 m, so far the maximum known depth. In most cases, the depth of cable damage exceeded 500 m, sometimes 1,000 m. Most often, the lower jaw and caudal fin of the sperm whales were entangled in the cable. It has been assumed that the whale held the cable in its mouth while chasing for food and then began to whip it when the slackened cable wound around it. It has been suggested that sperm whales become entangled at low depths and then gradually slip down along the slope of the sea bed. However, the nature of the entanglements revealed that they occurred at the places where the animals were actually found (Khizen,

1957; Yablokov, 1962). Sperm whales perhaps are actually capable of descending to a depth of 1,000 m or more.

After prolonged residence under water, the sperm whale rests a long time on the surface (Fig. 353). At this time, it remains almost stationary, only slightly moving forward; in a horizontal position, it rhythmically submerges and blows every 10 to 15 sec. The number of blows varies and probably depends largely on the time spent under water. Usually there are 20 to 40 blows but up to 75 in some cases. Compared to the older animals, the young ones produce fewer blows. The former evidently dive deeper and for a longer duration. During this characteristic rest period, the sperm whale remains very quiet and unconcerned, lying on the surface for 10 min or longer; in most cases, a whaling boat can approach such a whale within shooting range. During hunting around Antarctica there have been instances of a whaling boat literally approaching a sperm whale so close as to hit the animal with its stempost (V.A. Arsen'ev).

Sometimes a sperm whale rising from the deep emerges almost vertically from the water, thrusting about half of its trunk clear. In other cases, the animal leaps high at an angle to the sea surface and falls on the water with a loud splash.

The speed of the sperm whale is comparatively slow. The so-called moving or migrating whales (traveling from one region to another) usually travel straight at 5 to 7 miles/hr. They swim close to the water surface, often make shallow dives, and produce many blows. Feeding

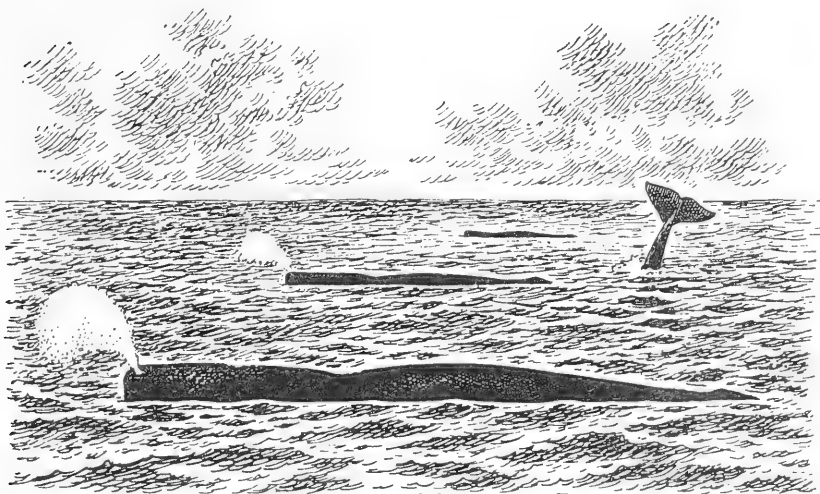


Fig. 353. Sperm whales at sea (figure by N.N. Kondakov).

animals move more slowly, probably at not more than 3 miles/hr. When searching for food, they remain submerged a long time, changing course under water regularly and very sharply. A frightened or wounded sperm whale moves at maximum speed, quite often along a straight course, and produces blows frequently. The maximum speed of a large sperm whale hardly exceeds 10 miles/hr. In any case, ships covering 12-12.5 miles/hr invariably overtake an escaping sperm whale after 40-50 min of pursuit.

A sperm whale wounded by a harpoon sharply dives deep but soon reemerges on the surface, rising almost vertically, and displaying its huge obtuse head. If the movement of the whale boat is not arrested in time, the surfacing whale can appear underneath it and damage the bottom severely by colliding against it with its head. Instances are known of such situations wherein the whale damaged the whaling boat by distorting the propeller blades or even the crest of the shaft. These cases formed the basis for the widespread belief that a wounded sperm whale often actively attacks a ship. Such attacks are no doubt unintentional and inflicted at random by the surfacing sperm whales (V.A. Arsen'ev).

Instances of sperm whales being beached, either singly or in groups, are not infrequent along the coasts of Denmark, France, Florida, California, Tasmania, and New Zealand. Eight cases have been registered of groups of beached whales ranging from 16 to 36 animals. Sometimes

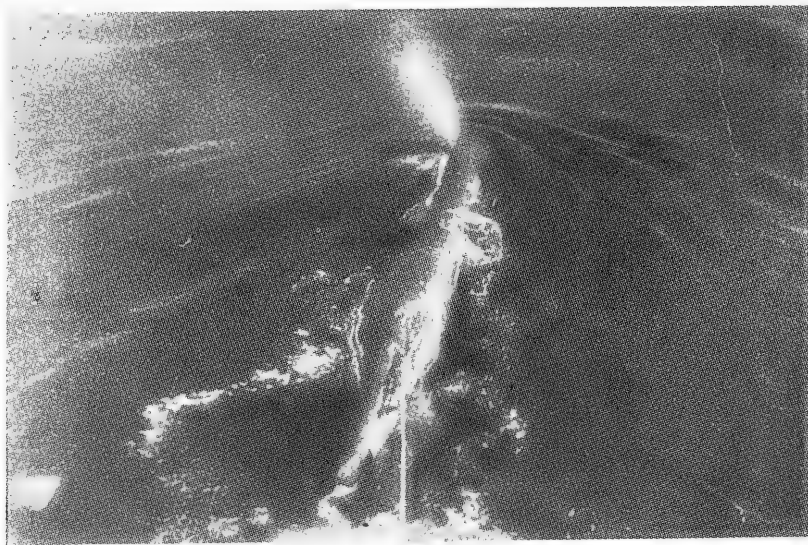


Fig. 354. Typical blows of the sperm whale. Pacific Ocean (photograph by M.M. Sleptsov).

such groups consisted exclusively of females but often of lone males. Twenty-two males cast up on January 16, 1954 on the coast of California were roughly identical in size (Gilmore, 1957; Tomilin, 1962) (Fig. 355).

Seasonal migrations and transgressions. The nature and courses of migration of sperm whales have not been thoroughly studied. The scheme of migrations is generally as follows: in the winter months, most of the sperm whales gather in warm and tropical waters and move in summer into temperate waters, although some males even depart into the cold waters of the Northern and Southern hemispheres. The main factor determining the courses of migrations and the distance of travel of sperm whales in cold waters is the effect of such currents as the Kuroshio in the Pacific Ocean and the Gulf Stream in the Atlantic. The zone of influence of these currents provides favorable conditions for the survival of the main food objects of the sperm whale, i.e., cephalopods, whose entry into the north in summer months is determined by the intensity and direction of the currents. Sperm whales move into relatively high latitudes in pursuit of these cephalopods.

Early in spring, in the North Pacific Ocean, sperm whales begin to migrate from the warm waters northward. Around the Bonin Islands the first females are sighted February end and by March their catch is maximum. Most of the whales migrate along the eastern coast of Japan. Some whales migrate northwest and are caught in small numbers on the western coast of Kyushu Island. They are sometimes encountered in the East China Sea. Sperm whales are not caught off the Korean coasts but



613 Fig. 355. A group of beached sperm whales. California (from R.M. Gilmore, 1956).

some numbers enter the Sea of Japan from the south (Omura, 1950). Some lone sperm whales, quite rare in fact, are noticed in Peter the Great Gulf and sometimes transgress even into the Bay of Zoloti Rog (Vladivostok). In the waters of southern Japan, sperm whales are seen early in spring, up to April; the earliest to arrive here are young, already mature males. In June-July, most of the sperm whale herds concentrate in the waters of Japan; at this time, males, females, and calves live here. In July, they move northward but the groups break up in the waters north of 45° N lat. Males separate from the general groups and go northward while females with calves inhabit the much warmer waters. The hunting of sperm whales in the waters of Japan is most fruitful from June through November (Nishiwaki, 1966).

In the central part of the Kuril range, the first sperm whales, exceptionally large single males, are sighted early in April and groups begin arriving by May. By mid-May, herds of sperm whales do not actually transgress north of the 48th parallel.

611 In the northern part of the Kuril range, lone male sperm whales are seen at April end to early May and by May end the so-called harem whales begin to arrive. By mid-June, stable collections, called herds, of sperm whales of different sexes and ages are formed here. Large males by this time move farther northward in large numbers (Tarasevich, 1965). In the first half of June, mixed groups of sperm whales are fairly uniformly distributed from the Pacific Ocean side of the middle and northern sections of the Kuril range and their herds depart farther from the coasts. Adult lone males by this time are seen in the Sea of Okhotsk, which is not at all visited by females or young animals. In July, the number of sperm whales around the Kuril Islands is far smaller and only minimal groups are seen throughout the region. It can be assumed that herds of sperm whales often travel at this time toward southeastern Kamchatka and are partly scattered over this immense water body.

At the end of July in the central part of the Kuril range (Bussol Strait-Simushir Island), new herds of sperm whales of medium size, consisting mainly of young males, are seen approaching from the south. At the very end of July, new herds are again seen in the region of Urup—Simushir. These herds contain many females and some large males. These are clearly the returning harems. During the first 20 days of August sperm whales remain in this region, even slightly extending southward (up to Friza Strait), but do not advance northward at all. At this time herds consist of very small animals but large whales begin to be sighted again by the end of August. They probably now begin to move out of the Sea of Okhotsk southward.

This pattern of arrivals confirms the assumption that during summer two narrowly localized sperm whale herds, i.e., southern Kuril and northern Kuril populations, inhabit the Kuril Islands. Whales of the southern Kuril herd inhabit the northern parts of the Japanese Islands and the southern parts of the Kuril range, reaching its middle in the north. The northern Kuril herd inhabits the waters of the northern Kuril Islands and is confined to the coasts of southeastern Kamchatka but may reach the waters of the Commander Islands (S.K. Klumov).

In September, the maximum number of sperm whales is seen in the Kuril waters since the whales returning from the northern waters now begin to arrive. October is the month of en masse departure of sperm whales southward and their herds around the Kuril Islands gradually thin out. Individual animals or even small groups may, in favorable years, remain for wintering close to the Kuril range (Sleptsov, 1955).

The northern boundary of distribution of adult females and young sperm whales of both sexes is regarded as 51° N lat. (Omura, 1950) although they are encountered even farther north, up to $52-54^{\circ}$ N lat. in Kronotskiy and Kamchatka straits and around the Commander Islands (Kirpichnikov, 1950b; Sleptsov, 1950; Tomilin, 1957). Hence, in favorable years, females can reach even up to $53-54^{\circ}$ N lat. The usual boundary of distribution of adult males is $61-62^{\circ}$ N lat. (Cape Navarin) where whales from both the western and eastern coasts of the Pacific Ocean live. It is more probable that the region of Olyutorskiy Gulf (60° N lat.) serves as the northern boundary of distribution for males of the Asian herd although some stray whales have reached $65^{\circ}30'$ N lat. under favorable conditions (Omura, 1950).

Migrations of the sperm whales of the American herd are as follows. From the wintering regions, disposed along a tentative line from the Hawaiian Islands to the coast of California, sperm whales begin to migrate northward at March end to early April. The period of migrations is considerably prolonged and hence they are sighted even in May in the southern parts of the range. The large extent of the wintering range along the longitude makes for several courses of migrations. One group moves along the coasts of the American mainland, another moves within $145-150^{\circ}$ W long., and yet another between 162 and 167° W long. In April or early May, all these groups reach roughly 50° N lat. where the comparatively linear course takes a complex route. At these latitudes the males from the mixed groups finally separate out, with some animals moving into the middle and eastern sections of the Gulf of Alaska and the Pacific waters of the Aleutian range, and others occupying the northernmost part of the Gulf of Alaska, moving far westward right up to the Commander Islands, entering the Aleutian Straits into the Bering

Sea (Bristol Bay and Pribilof Islands) and, spreading along the eastern shallow-water section of the sea, reach Cape Navarin and the Gulf of Anadyr. These are exclusively males of various dimensions and ages which gradually isolate from the mixed herds and gather in the regions of food concentration, at times forming significant herds. It has been assumed that the much younger, although sexually mature males are the first to separate from the common herds, followed by the larger older animals. This is possibly associated with the concluding phase of reproduction. The northern boundary of distribution of groups of females and young animals in all probability is $50-51^{\circ}$ N lat. They are confined predominantly to the Gulf of Alaska but are not infrequent in these same latitudes around the Aleutian Islands, sometimes reach the western section of the range and, more rarely, even the Commander Islands. Under favorable conditions, in some years small groups penetrate even farther north and are seen in the Bering Sea (Berzin and Rovnin, 1966; Tarasevich, 1967a).

The return of groups of sperm whales to the wintering regions commences in September. The sequence and periods of migrations of individual age and sex groups have not been unraveled. Migrations probably occur by the same routes as when moving northward. In November, the sperm whales practically abandon the northern regions of the range although some stray animals or small groups may overwinter there. Such instances are known even in the waters of the Commander Islands. Sperm whales reside almost everywhere around the central and southern Kuril Islands, and sometimes comparatively large herds are seen here in winter. Wintering sperm whales have been recorded even in the Gulf of Alaska (Zenkovich, 1936b, 1952; Sleptsov, 1955; Tomilin, 1957).

613 The periods of migrations of sperm whales in the North Atlantic are roughly the same as in the Pacific Ocean. After overwintering in the southern regions of the range, the whales begin to move north along the western and eastern coasts of the ocean in early spring. Mixed groups of sperm whales probably do not proceed north of 50° N lat. but mature males of different ages reach Iceland, Greenland, Davis Strait, and Jan Mayen and Spitsbergen islands. This is somewhat more northward than in the Pacific Ocean due to the influence of powerful Gulf Stream currents. Some males, depending on hydrological and trophic conditions, may sometimes overwinter in the north but most of the whales return to the southern waters in autumn.

Regular seasonal migrations are also known among populations of the Southern hemisphere but their extent differs for mixed groups and adult males. Mixed herds of sperm whales apparently do not travel beyond the south 40° latitudes since only one case has been recorded of a

female sperm whale being caught off South Georgia Island ($54^{\circ}30' \text{ S lat.}$). In the summer months, however, males are widely distributed in the waters of Antarctica and reach the ice there—which is not the case in the Northern hemisphere. In autumn males abandon the Antarctic Zone and return to their points of wintering. Sperm whales have not been observed at any time of the year in the Gulf of Guinea (Kirpichnikov, 1949b, 1950b).

Observations over several years in the various zones of the Southern hemisphere revealed that groups of small sperm whales, consisting of immature males and females as well as adult females, remained mainly in tropical waters. Large males were quite rare among them. The approximate body length of the small sperm whales was 7 to 10 m.

In the subtropical zone small groups of sperm whales, consisting of males that had attained sexual maturity but were still not participating in reproduction (approximate body length 12.0–12.5 m), were found. Groups of males about to attain maturity (body length 11.0–11.5 m) were encountered separately. The large males here were larger than in the tropical region but nevertheless constituted an insignificant minority.

In the zone of temperate waters (40° latitudes) there were no immature males or small whales measuring 7–8 m in body length. Mature males 12–13 m long predominated while large males constituted up to 20% of the total strength.

In the Antarctic waters (south of the 50th parallel), only large males 14–15 m long or more were encountered. Females and young sperm whales of either sex were totally absent (Tormosov, 1970).

Reproduction. Female sperm whales usually do not emerge beyond the warm and temperate waters and hence the seasons of mating and parturition among them are not as sharply manifest as among those whales whose females perform regular migrations into the cold waters of both hemispheres. Births occur among sperm whales throughout the
 614 year but the maximum number occurs in a relatively brief period. For the Northern hemisphere, this evidently is the early autumn months. In the North Atlantic, more births have been recorded from May through November with the maximum number taking place from July through September (Clarke, 1956).

On the eve of parturition, females concentrate in quiet zones where conditions are more favorable for the newborn. Such zones in the Pacific Ocean are the waters of the Marshall and Bonin islands, eastern coast of Japan, and to a lesser extent the waters of the southern Kuril Islands and the Galapagos Islands; in the Atlantic Ocean these are the waters of the Azores and Bermuda islands and the coasts of the African provinces of Natal and Madagascar. Sperm whales gather in regions with clean deep

water on the leeward side of islands or reefs (Sleptsov, 1955; Tomilin, 1957).

In the Southern hemisphere, births occur from December through April with a maximum in February. They take place in regions of quiet and relatively warm waters, where sharks, killer whales, and other enemies of the newborn sperm whales are few. The optimum water surface temperature would seem to be 15-17°C. For the Atlantic and Indian oceans, such waters are found between 35 and 39° S lat. and it is here that the majority of female sperm whales undergo parturition.

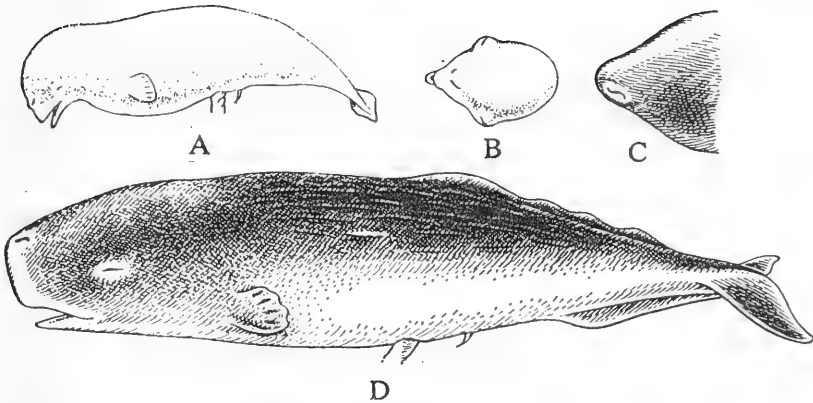
In April, 1962, close to Tristan da Cunha Islands, the process of parturition was observed from a helicopter (F. Khomchik). Among several groups of sperm whales, numbering 25-30 animals each, one group of six was obviously isolated. These whales dived continuously together in a row, churning the water, which soon became blood-stained and a newborn whale was shortly sighted on the water surface. The newborn immediately began to swim alongside its mother. The two were accompanied by four other sperm whales, probably also females.

Observers have noted that during birth the female assumes a vertical posture with almost one-quarter of the body length projecting above the water. The caudal flukes in the newborn remain coiled for sometime in the form of a small tube. Other adult females dive under the newborn calf and help it to remain afloat on the sea surface until the caudal flukes unfold (Tormosov, 1970).

Gestation in the sperm whale is far more prolonged than in most of the other species of cetaceans. It has been assumed to extend for 16-18 months (Matthews, 1938b; Nishiwaki, Hibiya, and Ohsumi, 1958; Ohsumi, 1965). The ratio of male to female embryos is close to 1:1. Of the 1,068 embryos studied in the northern part of the Pacific Ocean, males accounted for 48.1%. In the waters of Chile and Peru, of 1,118 embryos, males were 56.2% and in the waters of Africa (491 embryos) 45.6%. Of the total of 2,677 embryos studied, males accounted for 51.0% (Ohsumi, 1965). Females usually deliver a single calf; twins are very rare
 615 (0.66%, Clarke, 1956). The periodicity of reproduction has been put at three (Clarke, 1956) or even three to four years (Ohsumi, 1965).

Growth and development. Embryonic growth of the sperm whale continues for up to 16 (probably even 18) months. Thus the growth of embryos proceeds more slowly than among other species of whales, which are characterized by a very short period of embryonic growth (Fig. 356). The growth pattern of sperm whale embryos is depicted in Table 61.

The length of the newborn calves varies from 350 to 500 cm (Tomilin, 1957). The average size of the newborn from the North Atlantic is 392 cm (Clarke, 1956) and from the Southern hemisphere 415 cm (Lous,



614 Fig. 356. Embryonic growth of the sperm whale, *Physeter catodon* (figure by N.N. Kondakov).

615 Table 61. Growth of sperm whale embryos (in cm) (Ohsumi, 1965; Berzin, 1971)

Month of growth	Average length, according to	
	Ohsumi	Berzin
1st	6	10
2nd	24	20
3rd	52	30
4th	76	50
5th	103	70
6th	127	90
7th	155	115
8th	183	140
9th	210	170
10th	234	215
11th	262	260
12th	289	290
13th	314	320
14th	341	350
15th	369	380
16th	393	400

1959). The average size of calves, based on data for both hemispheres, is 405 cm (Ohsumi, 1965). The largest embryo from the North Pacific Ocean was 460 cm long (Berzin, 1964a). A newborn calf can weigh up to 1,000 kg.

The duration of milk suckling, on analogy with the other species of large whales, was initially considered to be 6-7 months (Vinogradov,

1949; Sleptsov, 1955), later 13 months (Clarke, 1956), but according to the latest data, 24-25 months (Ohsumi, 1965).

The age of the sperm whale has been determined by the number of layers in the dentine formed as a result of seasonal metabolic variations associated with changing conditions of habitation. Right up to the filling up of the pulp cavity, two layers of dentine are laid every year: one very broad, light-colored, and intensely calcined, the other very narrow, dark-colored, and less calcined (Fig. 357). These two layers form a single annual ring whose number reflects the age of the whale (Nishiwaki, Hibiya, and Ohsumi, 1958; Berzin, 1961). The question of the number of layers laid in the course of a single year has not yet produced a commonly accepted opinion. It is possible that the annual rings may be two, or a single annual ring may consist of different numbers of intermediate rings. This aspect continues to be studied.

By the end of the first year, sperm whales of the North Pacific Ocean reach a length of 6 m or slightly more, i.e., the increment in body length at the end of the first year is almost 2 m (all figures are average values). The growth tempo subsequently slows down somewhat and by the third year the animal reaches a length of 8 m, adding another 2 m in these two years. By age 3.5-4 years, the female sperm whales have attained sexual maturity and their growth tempo subsequently is markedly slower than that of the males, with the annual increment not exceeding 50 cm. The onset of physical maturity and growth cessation among females occurs at the age of 15 years at a body length of 11 m. Females 11.7 m long are over 30 years of age and have already lost their middle pairs of

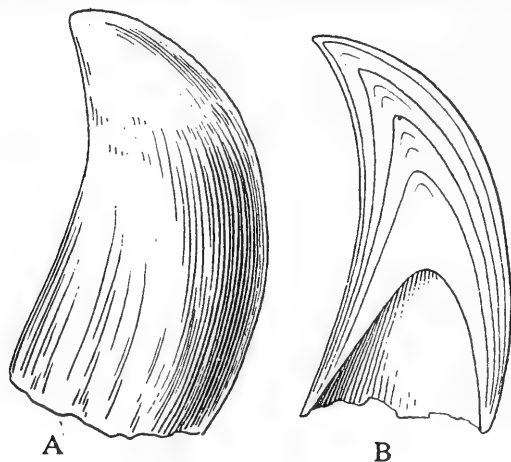


Fig. 357. Tooth of the sperm whale, *Physeter catodon*. A—external view; B—longitudinal section (figure by N.N. Kondakov).

616 teeth. It may tentatively be assumed that at maximum age females have attained a length of 12 m or slightly more. Males attain sexual maturity at 5 years of age and a body length of 9.5 m but their growth tempo subsequent to reaching sexual maturity does not decrease initially. For the next few years the annual increment averages 80 cm, then gradually decreases thereafter. Growth cessation is noticed at the age of 23-25 years at a body length of about 16 m (Berzin, 1961, 1964a). The body length of male antarctic sperm whales at the time of attaining sexual maturity is 11.5-12.5 m because of the generally larger dimensions of whales of the Southern hemisphere (Matthews, 1938b; Nishiwaki, 1955; see under "Geographic Variation").

Under conditions of intense contemporary hunting practices, the maximum length of male sperm whales very rarely reaches 18 m and whales larger than this size are not found at all. Age determination revealed the oldest females to be 30 years (body length 10.7 m), over 30 years (body length from 10.9 to 11.7 m), and over 35 years (11.1 and 12.4 m); males were 27 years (15.6 and 14.8 m), 29 years (16.2 m), and over 30 years (14.8 m) or even 32 years. It has been assumed that age determination of animals older than 35-40 years is not possible since the pulp cavity is totally sealed. Be that as it may, this age is not a maximum for the sperm whale (Berzin, 1971).

Enemies, diseases, parasites, mortality, and competitors. There is only one known case of a piece of the rostrum of a swordfish being found in the trunk of a beached sperm whale (Tomilin, 1957). Diseases have not been studied. Only dental caries, distortion of the lower jaw, and some other diseases are known.

A significant film of diatomaceous algae with *Cockoneis ceticola* predominating, has sometimes been observed on the body of the Antarctic sperm whales. In tropical waters minute ulcers have been detected on the skin of sperm whales, which form scars during the residence of the animals in the cold seas: the nature and origin of these ulcers are not understood. Crustaceans of *Penella* sp., common in rorqual, infect individual sperm whales occasionally. Barnacles are also rare and found in small numbers. They comprise three species of the genus *Conchoderma* (*C. auritum*, *C. virgatum*, and *C. cuvieri*). *Coronula* sp. has been encountered as a rare exception. The whale lice *Cyamus physeteris* and *C. catodontis* are common parasites of most sperm whales. They infest more often the urogenital and anal openings, less so the wrinkled flanks, and very rarely the dorsum (Clarke, 1956; Tomilin, 1957).

Thirty-one species of helminths are known in sperm whales. These include trematodes 1, cestodes 12, nematodes 10, and acanthocephalans 8 species. The single species of trematode, found in the Kuril waters,

Zalophotrema curilensis Gubanov, parasitizes the liver of only the sperm whale.

Of the 12 species of cestodes, 5 are found exclusively in sperm whales. *Tetrabothrium curilensis* Gubanov and *Hexagonoporus physeteris* Gubanov parasitize the small intestine and *Tetragonoporus calyptocephalus* A. Skrjabin localizes in the bile ducts of the liver; all three have been found in Kuril waters. *Multithuctus physeteris* Clarke parasitizes the bile ducts of the liver and *Polygonoporus giganticus* A. Skrjabin the intestine in
 617 the Antarctic. The cestode *Tetrabothrius affinis* Lönnberg, found in the waters of Norway, South Africa, New Zealand, and Antarctica, parasitizes the intestine of the sperm whale and three species of baleen whales. *Priapocephalus grandis* Nybelin was found in the intestine of the sperm whale and four species of baleen whales in the Pacific Ocean. *Phyllobothrium delphini* Bosk, parasitizing the skin and found at many places in the Atlantic Ocean, the Mediterranean Sea, waters of the Commander Islands, Australia, and Antarctica, has been detected in the sperm whale, six other species of toothed whales, Weddell seal, and the Arctic whale. Further, some cestodes not identified to species level, have been detected in the sperm whale. These are: species of Tetraphyllidae (larvae) in the subcutaneous adipose tissue, *Diplogonoporus* sp. in the bile ducts of the liver, *Trigonocotyle* sp. in the small intestine of the sperm whale and Baird's beaked whale, and *Trypanorhyncha* sp. (larvae) in the stomach of the sperm whale, sei whale, Minke whale, and Steller's sea lion.

Of the 10 species of nematodes, 5 are found exclusively in the sperm whale. The stomach parasite, *Anisakis (Anisakis) catodontis* Baylis, has been detected in the waters of South Africa; *Anisakis (Skrjabinisakis) physeteris* Baylis in the North Pacific Ocean, waters of South Africa, and Antarctica; and *Anisakis (Anisakis) ivanizkii* Mosgovoy around the Commander Islands. *Placentonema gigatissima* Gubanov was found in the placenta (Kuril Islands). *Anisakis (Skrjabinisakis) skrjabinii* Mosgovoy parasitizes the stomach and small intestine of the sperm whale and spotted dolphins (Commander Islands, Sea of Okhotsk, and Antarctica). *Anisakis (Anisakis) dussumierii* Beneden, parasite of the stomach and large intestine of the sperm whale and spotted dolphins, was detected in the waters of Japan and the Commander Islands. *Anisakis (Anisakis) simplex* Rudolphi, found in the sperm whale and widely distributed in marine mammals (North Sea, eastern Kamchatka, Japan, and New Zealand) parasitizes the gullet, stomach, and intestine. In the northwestern part of the Pacific Ocean, *Anisakis (Anisakis) pacificus* A. Skrjabin was detected in the stomach of the sperm whale, killer whale, and fin whale. Moreover, *Anisakidae* g. sp. and *Tetrarhynchidae* m. sp. (not identified to the species level) also parasitize the sperm whale.

Two species of acanthocephalans parasitize the intestine only of the sperm whale: *Corynosoma curilensis* Gubanov was found off the Kuril Islands and *Corynosoma mirabilia* A. Skrjabin in Antarctic waters. *Corynosoma strumosum* Rudolphi, parasite of the intestine, is known only in belugas, common porpoises, 11 species of pinnipeds, and land mammals and birds. *Bolbosoma physeteris* Gubanov was detected in the intestine of the sperm whale and the killer whale in the waters of the Kuril Islands. *Bolbosoma capitatum* Linstow parasitizes the intestine of the sperm whale and two more species of toothed whales from the Atlantic Ocean and the Mediterranean Sea. *Bolbosoma brevicolle* Malm, detected in the large intestine and rectum of the sperm whale, is also known in five species of baleen whales; it has been found in the North Atlantic, in the waters of South Africa, and near South Georgia Island. *Bolbosoma turbinella* Diesing parasitizes the intestine of the sperm whale, beaked whales, and five species of baleen whales from the Atlantic and Pacific oceans of the Northern and Southern hemispheres. Finally, *Bolbosoma tuberculata* A. Skrjabin, detected in the South Atlantic and Indian oceans, parasitizes the intestine of the sperm whale, sei whales, and Bryde whales (Margolis, 1954; Delamure, 1955; Margolis and Pika, 1955; A. Skrjabin, 1958, 1959, 1960, 1961, 1970; Berzin, 1971).

Natural mortality of the sperm whale has not been studied nor have the reasons for the death of besched whales been ascertained.

The sperm whale has almost no trophic competitors with the possible exception of members of the family of beaked whales.

Population dynamics. Population variations in sperm whales due to natural factors are not known but due to hunting are significant. Hunting of sperm whales using manual harpoons and sailboats commenced in the first half of the eighteenth century and continued over the next one hundred years on an extensive scale. By the mid-nineteenth century, sperm whale reserves had shrunk markedly in all the seas; hunting became unprofitable and almost ceased. This promoted a significant restoration of the reserves of the sperm whale.

The second stage in sperm whale hunting commenced with modern techniques using whaling fleets and reached a high magnitude. As a result, by the 1960s there was a sharp reduction in the population of sperm whales in some regions, accompanied by a reduction in the average size of the animals caught, increase in the relative number of much younger animals in the catch, and some other features of diminishing reserves. This situation was mainly noticed in the waters of Japan and the Kuril Islands and to a lesser extent in the other regions, including the Antarctic where only adult male sperm whales that have not participated in reproduction are known to gather.

Field characteristics. The huge angular head occupies over one-third of the body length. The blowhole in the sperm whale is at the end of the snout on the left side and not on the upper part of the head, as in all other whales; hence the blow of this animal is not vertical but set forward to the left at an angle of roughly 45° to horizontal. The blow is broad, "bushy," with a height of not more than 3-4 m. The sperm whale can be recognized with certainty from a distance by the nature of the blow. The body color is monochromatic, usually dark. While diving to a depth it often exhibits the caudal flukes. After prolonged submergence, it lies on the water surface almost without movement and allows the very close approach of ships. (V.A.)

Economic Importance

The development of sperm whale hunting intensified mideighteenth century following the rapid decline of the catch of right whales whose herds had been destroyed. Hundreds of sailboats, working mainly in the tropical waters of all the three oceans, i.e., predominantly in the reproduction sites of sperm whales, were engaged in hunting them. This hunting proved highly profitable since the demand for spermaceti was inexhaustible and its price very high. Spermaceti was used mainly in the candle-making industry: candles made from it burn with a bright flame and without soot. By the mid-nineteenth century, kerosens was being used for illumination and the demand for spermaceti fell sharply. By this time a perceptible reduction in number of sperm whales had also made hunting unprofitable and it almost ceased circa 1860. The let up in hunting of the sperm whale continued for about half a century.

Early in the twentieth century, the hunting of sperm whales (mechanized by now) was resumed. It was particularly well developed in the North Pacific Ocean, along the coasts of South America, and later even in the Antarctic. Following the reduction in the population of the main commercial species of baleen whales, the importance of the sperm whale rose gradually in all the regions of the World Ocean although not to the same extent everywhere.

In the North Atlantic Ocean the sperm whale is of utmost commercial importance in the southern part of the range. Thus in the Azores it represents a unique commercial species of whale. From the end of the 1930s to the end of the 1950s, 500 to 700 sperm whales were caught annually. From the beginning of the 1960s, the volume of hunting decreased somewhat—from 400 initially to 300 whales later to 145 in 1969. Around Madeira Island, too, the sperm whale was caught exclusively but the magnitude of hunting was relatively small. Commencing from the early 1940s,

the catch did not exceed 200 a year and after 1967 did not reach even 100.

619 This species is of some commercial importance in the whaling industry of Spain, Portugal, and the northern part of western Africa where sperm whales have accounted in some years for 30 to 80-90% of the 200 to 300 whales caught annually. In the northern waters these whales are of some importance in Norway and Iceland although the number caught is small. On the Norwegian coasts no more than a hundred sperm whales are caught per year, or 15 to 40-50% of the total catch; they numbered 120-170 animals per year or 25-45% of the total catch in the waters of Iceland from the end of the 1950s to the mid-1960s. At the end of the 1960s, the annual catch was 100 sperm whales.

The more abundant sperm whale population of the North Pacific Ocean ensures a larger catch. The catch is particularly high in the coastal stations of Japan and from large floating whaling stations. Up to 1950, less than 1,000 sperm whales were caught off the coasts of Japan, which represented about half the total catch of whales of all species. From 1950, hunting activity rose considerably and the number of sperm whales caught ranged between 1,200 and 2,600 animals per year. In 1968, the sperm whales caught here numbered 3,747 and in 1969—3,668. In some years sperm whales accounted for 60-70% or even more of the total catch. Until the mid-1950s, when the "pelagic" fleet was not large, the catch of sperm whales usually did not exceed 500-700 animals per annum. But from the mid-1950s, with the introduction of new Soviet and Japanese whaling fleets, it began to rise rapidly: initially up to 2,000 and then 4,000, reaching almost 8,000 sperm whales a year by the early 1960s. Between 1965 and 1969, the number of sperm whales caught totaled 10,500 to 12,500 per year or 50-70% of the total catch of the fleet. Sperm whales caught from the coastal bases on the Kuril Islands between 1950 and 1962 totaled 1,400 to 2,000 (70-80% of the total catch). The whaling industry of the Kuril Islands came to a halt in 1964. Large-scale hunting of sperm whales in the northeastern part of the Pacific Ocean also ceased. From the coastal bases of British Columbia, from the end of the 1940s to the early 1960s, 120 to 320 sperm whales were caught per year but whale hunting ceased in 1967. Off the coasts of California, the catch never exceeded a few tens (sometimes up to a hundred) of sperm whales per year.

The sperm whale catch in the Southern hemisphere has been large with several areas participating in the hunt: waters of Chile, Peru, South Africa, pelagic hunting in the Antarctic, and, in recent years, in the more northern waters. In the African waters (Natal and Cape Province) whale hunting was resumed in 1948 and 400 to 1,000 sperm whales of a total of 1,200 to 2,700 whales were caught every year until 1956. From 1957,

the catch of sperm whales increased considerably and 1,200, 2,500, and even 3,600 sperm whales were caught every year (50-70% of the total catch). Off the coasts of Chile and Peru, sperm whales represented the main species of whales hunted and accounted for 70.9 and even 100% of the catch. The maximum number of these whales caught from the mid-1950s to the mid-1960s ranged from 2,500 to 5,000 animals per year. At the end of the 1960s, hunting fell slightly to less than 2,000 animals. After the Second World War, the "pelagic" whaling fleet of the Antarctic developed rapidly and caught a large number of sperm whales (exceptionally large males). But, of the 2,000-4,000 to 6,000-7,000 animals caught, sperm whales in a season constituted only 10-15% and later 20-22% of the total catch of the whaling fleet. From 1967 to 1969, the catch of sperm whales in the Antarctic fell to 2,500 to 2,600 animals per year but the Antarctic whaling fleet began catching these whales north of 40° S lat. along the course into Antarctica and back. This catch accounted for 2,000 or more sperm whales in a season. In Australia hunting of the sperm whale commenced only in the mid-1950s, following a reduction in the population and subsequent total ban of hunting of humpback whales (these were the lone target of hunting in these waters). From the mid-1960s, the number of sperm whales caught in Australian waters totaled 500 to 600 per year.

620 Modern hunting of sperm whales, like that of other large whales, is carried out in special steel ships equipped with harpoon guns. The whale is killed with a harpoon with a grenade screwed to its tip and primed with gun powder. The grenade fires 4 sec after shooting and by this time the harpoon has penetrated the whale body (Fig. 358). The firing can be fatal or otherwise depending on the resistance of that part of the trunk struck by the harpoon. The wounded whale is dragged toward the boat by a rope tied to the harpoon, using a special winch, and the animal finally killed by shooting a second (or third) time. Instances of a whale requiring up to six shots are known.

The behavioral aspects of the sperm whale make for some typical features in hunting them. After prolonged submergence, the sperm whale usually remains a long time on the sea surface. This facilitates the approach of the ship within shooting range while the animal's attempt to escapeton a straight course enables the chasing whale boat to catch up with it quickly. Thus most of the sperm whales sighted from the ship can be killed. But if the marked sperm whale succeeds in diving before the ship can approach, it is futile to wait for it to surface again.

Air is pumped into the body cavity of the killed sperm whale so that the carcass floats and can be towed to the floating base or the coastal station for dressing. First the blubber is removed in layers and then the

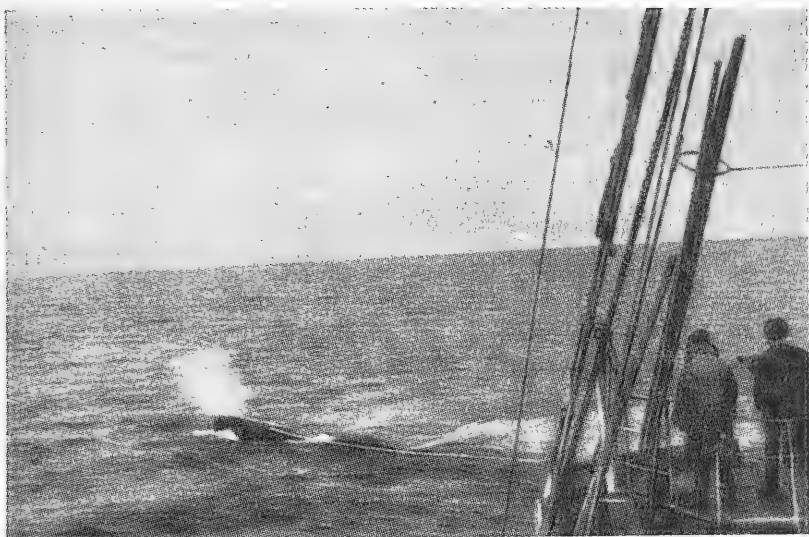


Fig. 358. Harpooned sperm whale (photograph by V.A. Arsen'ev).

head is severed from the trunk. Using a steam or electric hoist, the large stock of fat in the spermaceti sac is recovered, sliced into large lumps, then charged into a boiler for melting the spermaceti. Then the viscera are removed from the carcass and the flesh from the bones. The bones of the skeleton and skull are cut by steam-powered saws into bits that can be fed into fat-melting boilers to ensure more complete conversion into oil.

The main product obtained from the sperm whale (Table 62) is the oil from the blubber, bones, and viscera. The physical and chemical properties of the oil of the sperm whale differ from those of baleen whales (low specific gravity, low saponification number, low iodine number, etc.). The oil is used for commercial purposes by various industries. A large male (length 14-16 m), on average, yields about 10 tons of fat. Spermaceti has a characteristic chemical composition and is collected and processed separately from the blubber. Spermaceti is used by perfumeries in preparing cosmetic media (creams and pomades) and to a lesser extent in other industries as well. The liver of the sperm whale contains the maximum amount of vitamin A compared to the liver of all other species of whales: about 6,000 units, on average, versus 1,500 units in a female fin whale (Mrochkov, 1953). The mechanical method of pressing the subcutaneous fat layer yields more oil than digesting in a boiler (Dormenko, 1952; Zaikin, 1953). In the former method the upper

layers of the integument can be used in making leather goods. For this purpose two layers of 5-6 mm thickness each are taken from the carcass of the whale and a third additional layer up to 8 mm thick from its head. Much deeper layers can also be used in the leather industry but only after special compaction using special fillers.

Table 62. Weight of the body parts of the sperm whale, kg (Zenkovich, 1937b; M.V. Ivashin)

Body part	Far East (Kronotsk Bay)		Antarctica
	Male 13.5 m	Male 18.0 m	Male 16.1 m
Subcutaneous fat	4,955	12,663	11,450
Spermaceti	620	5,757	4,400
Spermaceti sac	3,981	10,343	8,665
Flesh	5,640	7,697	7,850
Skull	1,800	6,087	4,100
Lower jaw	320	880	1,050 ¹
Vertebral column	1,986	3,387	3,455 ²
Caudal flukes	314	715	
Ribs	965	2,147	3,290 ³
Flippers	485	978	
Pelvic bones	108	200	
Sternum	209	329	
Viscera	1,282	2,199	3,340
Total	22,665	53,365	47,600
Liver	—	—	620
Liver and kidney	331	368	—
Heart	113	211	—
Lungs	161	317	—
Lungs, heart, neck, and gullet	—	—	1,300
Stomach and intestine	—	—	700
Intestine	254	465	—
Testes	10.5	16.5	—
Penis	88	106	—
Remaining parts	323	716	720

¹Lower jaw together with tongue.

²Vertebral column together with caudal flukes.

³Ribs together with flippers.

Length of whale, m	Area of raw skin, m ²
8.9	19.2
9.5	25.5
10.5	28.4
11.0	33.0
14.5	55.5
15.3	71.0

622 Soles made from the skin of the sperm whale are not inferior (sometimes even superior) in wearing properties to those made from cattle hide. However, the skin of the sperm whale always suffers from defects, such as flaws of 5-10 mm in diameter and scars and scabs sometimes up to 50 cm² or more in area. As these damages are randomly scattered all over the skin, cutting is difficult and much wastage results (Bulgakov *et al.*, 1954). Hence the use of sperm whale skin in making leather goods has not developed. The lower layers of the skin, after mechanical degreasing, can be used in making gelatin and glue (Kolchev, 1954). The teeth of the sperm whale are excellent material for carved articles (chess pieces, handles, etc.) and almost indistinguishable from those made of ivory.

Sperm whales carry ambergris in the form of a hard waxlike substance present in large lumps of indeterminate form. Crude ambergris varies from gray to black and smells like wet soil. It has a granular and layered structure. Its specific gravity varies from 0.730 to 0.780; it softens from the warmth of the hand, melts at 60°C without bubbling, and volatilizes at 100°C. It dissolves well in hot alcohol and burns with a light blue flame and slight resinous smell.

Although ambergris is known from ancient times, its origin has yet to be ascertained. It is sometimes found floating on the water or cast on seashores. In the remote past it was regarded either as refuse of birds or as an exudation of plants and roots of trees. Later, the remains of chitinous "beaks" of cephalopods consumed by the sperm whale were detected in the ambergris, which suggested its origin from the intestinal tract of the whale. Its formation is thought to be a reaction to infection by parasites inhabiting the intestine or a product of the normal secretion of the rectal glands. The third point of view would appear to be more correct, according to which ambergris is formed as a result of the retention of undigested remnants of "beaks" of cephalopods, which are enveloped in special secretions in the digestive tract of the sperm whale.

Depending on its quality, ambergris costs 150-200 rubles per kg. The production of synthetic ambergris has somewhat affected the cost of the natural product but the quality of the synthetic is inferior to the natural. In olden times ambergris was used as an antispasmodic and in Chinese medicine as a stimulant or antiseptic. The chief value of ambergris lies in its exclusive property of absorbing odor and exceptional retention of it. Therefore, natural ambergris is used in producing perfumes of superior quality.

Ambergris is found in the intestinal tract of sperm whales in lumps weighing several hundreds of grams to tens of kilograms. Remarkably large lumps of ambergris have also been found: one lump weighing 392 kg was recovered in the Azores and another weighing 420 kg off the coast of

Australia. In our country a lump of ambergris weighing 351 kg was recovered in 1958. In subsequent years, ambergris production has exceeded 3 tons (Ivashin, 1966). Ambergris as a raw material requires sometime for maturation and hence all varieties of ambergris do not command the same price and some are even totally unsuitable for use in perfumeries.

Following the conclusion of the International Whaling Convention, 1946, some restrictions were imposed on the hunting of sperm whales. According to the international hunting rules, killing of sperm whales less than 10.7 m long was prohibited from the coastal whaling stations and less than 11.6 m long from the floating fleets, even though many sperm whales of these sizes are mature animals. In spite of these restrictions, highly intense sperm whale hunting continued and enormous catches led to a steady depletion in numbers, especially in the better exploited populations. Now a restriction has been imposed on killing sperm whales by prescribing annual quotas in all parts of the World Ocean, taking into consideration the strength of individual populations. In most cases, it would be extremely useful to restrict the killing exclusively to male sperm whales which, given the prevailing polygamous mode of life of these whales, could not adversely affect the normal replenishment of the various populations. (V.A.)

Subfamily of Dwarf Sperm Whales

Subfamily KOGIINAE Gill, 1871

Genus of Dwarf Sperm Whales

Genus *Kogia* Gray, 1846

1846. *Kogia*. Gray. Zoology of the Voyage of H.M.S. Erebus and Terror, I, p. 22. *Physeter breviceps* Blainville.

1876. *Cogia*. Wallace. Geogr. Distr. Anim., 2, p. 208. Correction of *Kogia* Gray. Nom praeocc. (V.H.)

Dimensions the smallest in the family, with a total length up to 3.4 m.

The body form is dolphin-shaped. The head is small, proportional, constitutes 1/8th to 1/6th of the body length, and is rounded anteriorly. The spermaceti sac⁵ is well developed on the head but much smaller than in the sperm whale. The blowhole is situated on the parietal section of the head, almost at its center. The blowhole opening is crescent-shaped. The end of the lower jaw falls far short of the anterior end of the head. The fairly high dorsal fin lies roughly midbody. The flippers are relatively

⁵ See description under sperm whale, p. 799.

narrow and short. The body is dark-colored dorsally and light-colored ventrally.

The rostrum is broad at the base, constricted sharply in the anterior part, and is shorter than the cranium. The depression on its dorsal surface is small and has a longitudinal crest formed by the premaxillae and maxillae. The nasal bones are not fused with the premaxillae. The maxillae have very large preorbital processes. The zygomatic bone does not articulate with the squamosal. The symphysis of the lower jaw is shorter than half its length.

Teeth: 8-16 pairs on the lower jaw and 1-3 pairs in the anterior section of the upper jaw (but sometimes totally absent in the latter). They are thin, curved, and the sharp tip set posteriorly. Enamel is absent.

Vertebrae 52-57: cervical 7, thoracic 12-14, lumbar 9-12, and caudal 21-27. The cervical vertebrae are fused. The flattened scapula has a small acromion and large coracoid processes. Ribs 13-14 pairs. The sternum is short. The phalangeal formula in the forelimbs is subject to individual variation: I_2 , II_{5-8} , III_{4-8} , IV_{4-8} , and V_{2-7} .

The population of the dwarf sperm whale is small. Biology has not been well studied. It lives singly or in small groups and apparently feeds mainly on cephalopods. The periods of mating and parturition are protracted. Gestation continues for about nine months. Females evidently reproduce annually. They live in the warm waters of the Indian, Atlantic, and Pacific oceans (Fig. 359).

There is no special hunting of dwarf sperm whales in view of their rarity.

The genus comprises two species (Handley, 1966): 1) dwarf sperm whale, *Kogia breviceps* Blainville, 1838; and 2) Owen's dwarf sperm whale, *Kogia simus* Owen, 1866.

Dwarf sperm whales are not observed in USSR waters but summer transgressions are possible (especially of Owen's dwarf sperm whale) into the Sea of Japan and toward the southern part of the Kuril Islands. (V.S.)

DWARF SPERM WHALE

Kogia breviceps Blainville, 1838

1838. *Physeter breviceps*. Blainville. Ann. Franç. étrag. d'Anatomie Physiol., 2, p. 337, pl. 10. Cape of Good Hope. (V.H.)

Diagnosis

Dimensions largest in the genus, with the overall body length varying from 2.7 to 3.4 m. The relatively low dorsal fin lies slightly posterior to

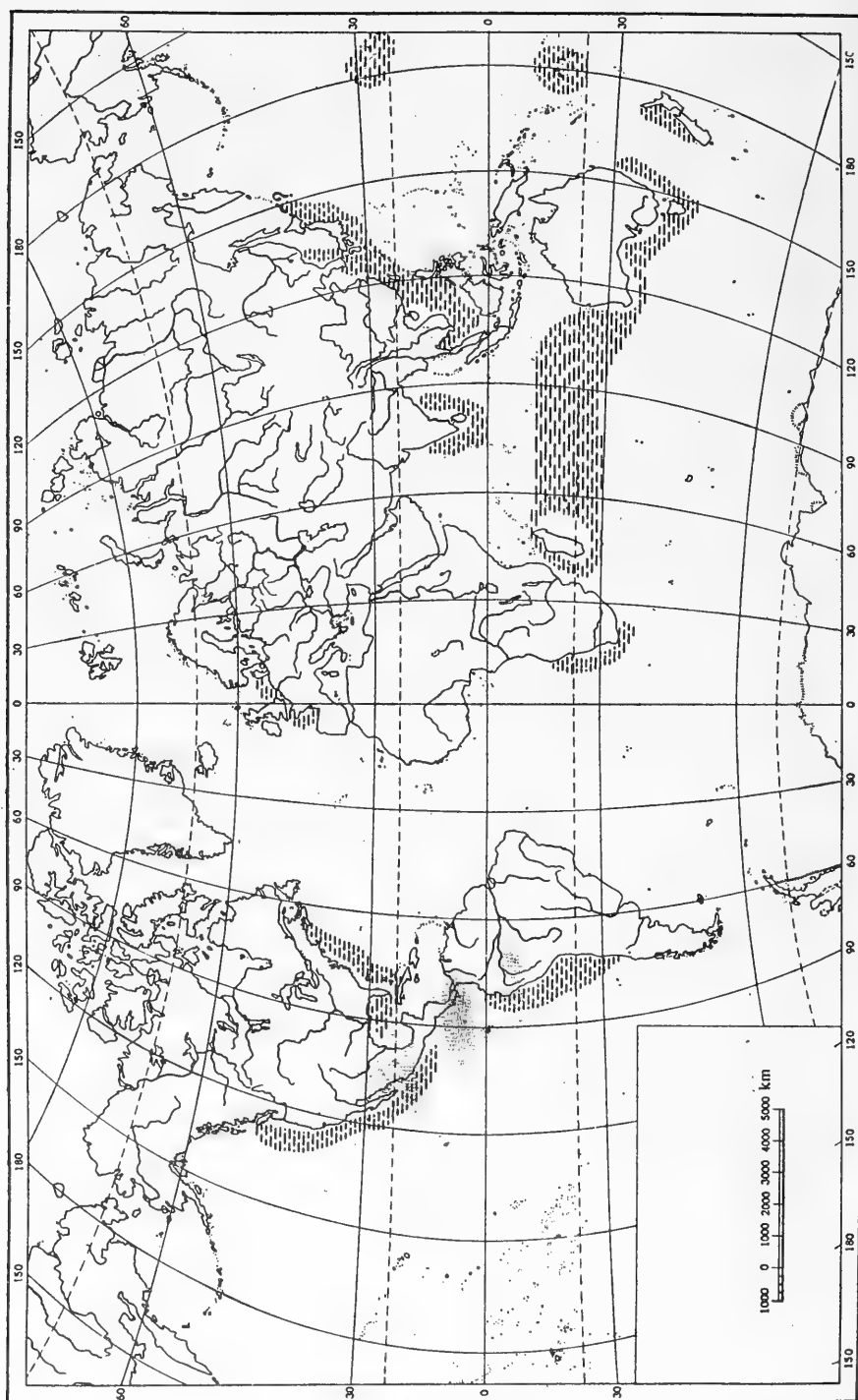


Fig. 359. Range of the genus of dwarf sperm whales, *Kogia* (V.A. Arsen'ev).

midbody. Teeth are absent in the upper jaw. Mandibular teeth 12-16 pairs (less frequently 10-11 pairs). (V.S.)

Description

The body dorsally, including the caudal flukes and flippers is dark, almost black. The flanks are light gray and the abdomen light-colored. Posterior to the eyes and anterior to the flippers, one or two light-colored projections run bottom upward into the dark-colored region (Fig. 360). Light-colored spots are visible on the ventral surface of the caudal flukes.

The body dimensions of adult male and female dwarf sperm whales from New Jersey and Texas states (USA) (Tomilin, 1957) are respectively (in cm): body length 299 and 274; distance from tip of snout to center of blowhole 32 and 35, up to anterior margin of dorsal fin 154 and 150; distance from anal opening to notch between caudal flukes 97; length of flippers 41 and 43; height of dorsal fin 9 and 13; length of dorsal fin 14 and 41; and width of caudal flukes (between apices) 50. The animals range in weight from 318 to 408 kg.

The condylobasal length of the skull (Fig. 361) is 391-469 mm. The mandibular symphysis is long (8.6-12 cm), with a keel on the ventral surface. The alae of the pterygoids and basioccipitals are elongated. The foramen magnum is situated roughly midpoint of the skull height. (V.S.)

Geographic Distribution and Biology

Inhabits predominantly the warm belt of the Pacific Atlantic, and Indian oceans. Distribution has been studied mainly from the finds of animals cast on coasts or shoals. More than 15 finds of beached dwarf sperm whales are known on the coasts of South Africa, Australia, and New Zealand, and over 50 on the Atlantic coast of the USA. Finds in the Pacific Ocean are not rare near Japan, the East China and South China seas, Gulf of Siam, along the coast of North America (Washington and

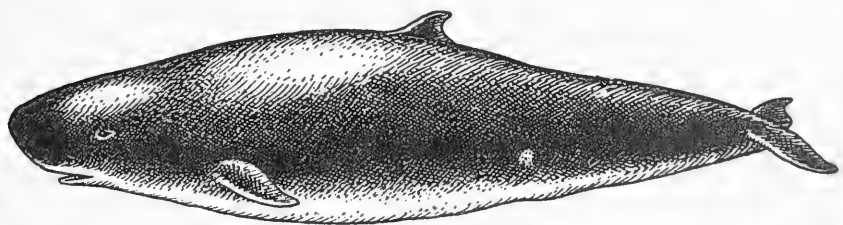
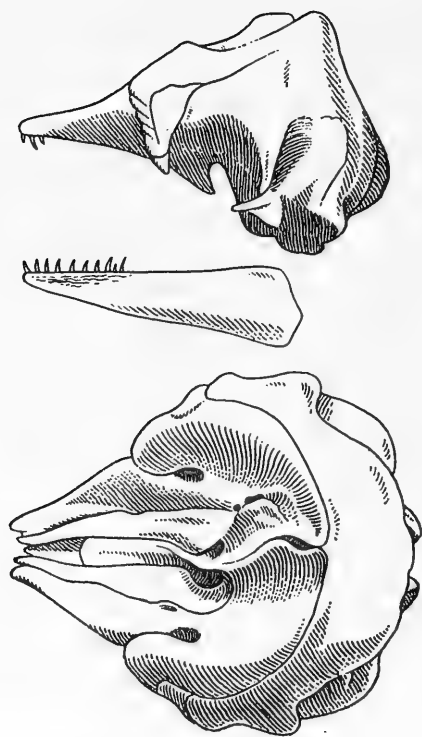


Fig. 360. Dwarf sperm whale, *Kogia breviceps* (figure by N.N. Kondakov).



625 Fig. 361. Skull of the dwarf sperm whale, *Kogia breviceps* (figure by N.N. Kondakov).

626 California states), and along the coasts of Mexico, Peru, Chile, Fiji Islands, Australia, Tasmania, and New Zealand. In the Indian Ocean, it is distributed from southern Australia to South Africa. In the Atlantic Ocean, beached animals are known on the coasts of North America from Nova Scotia to Florida and Texas, and on the coasts of South Africa, France, and Holland. In the Atlantic Ocean, these whales probably move into the open sea even in latitudes more northern than Holland (Dell, 1960; Tomilin, 1962; Gaskin, 1966; Hershkovitz, 1966; Handley, 1966).

The residence of these animals in the waters of the Soviet Union has not been established. Transgressions are possible in the summer months into the Sea of Japan and the southern part of the Kuril range.

Geographic variation of the species has not been studied.

Information on the biology of dwarf sperm whales is very fragmentary. Remains of cephalopods (*Sepia officinalis* and others) have been detected in their stomach. Cephalopods apparently serve as their main food. Bones and otoliths of fish (*Trichodon* sp. and others),

crabs (*Carcinides maenas*), shrimps (*Paciphola pacifica*, *Pandalus* sp., *Pandalopsis* sp., *Penaeus* sp., *Hymenodora* sp.) have been found less often.

The period of mating is greatly prolonged and newborns have been encountered even in November and February; however, the majority of these whales probably mate in summer. Gestation is thought to extend for 9-10 months. The length of a newborn calf is around 110 cm; whales 153-171 cm long were still suckling and a female with a body length of 188 cm was immature. Females attain sexual maturity at a body length of 218-219 cm. A female about 3 m long, beached on a Dutch coast in December, 1925, contained an embryo 20 cm long. Females give birth to a single calf. An instance is known of a female, accompanied by a small calf, who was simultaneously pregnant and lactating.

Dwarf sperm whales live singly, in pairs, or in small groups of up to five animals. Their movements are slow.

Penela sp. was found among the ectoparasites. Larvae of the cestodes *Monorygma grimaldii* Monier and *Phyllobothrium delphini* Bosk and the nematodes *Crassicauda magna* Jonston and Mawson and *Pseudoterranova mogiae* Jonston and Mawson, have been detected in the abdominal cavity and subcutaneous tissue.

A female 277 cm long weighed 369 kg while large males weighed up to 500 kg. There is no special hunting for these whales. The Japanese industry while catching various species of dolphins occasionally nets dwarf sperm whales also. Although their flesh is edible, these whales are not of economic importance (Delamure, 1955; Tomilin, 1957, 1962; Nishiwaki, 1965; Handley, 1966). (V.A.)

OWEN'S DWARF SPERM WHALE

Kogia simus Owen, 1866

1866. *Physeter (Euphyseter) simus*. Owen. Trans. Zool. Soc. London, 6 (I), p. 30, pls. 10-14. (V.A.)

Diagnosis

Dimensions the smallest in the genus, with overall length ranging from 2.1 to 2.7 m. The relatively high dorsal fin is roughly midbody. The upper jaw usually has 1-3 pairs of teeth and the lower 8-11 pairs (less often, 13 pairs). (V.S.)

Description

The body is dorsally dark gray and ventrally white.

The body measurements of a male and two females from Japan (Yamada, 1954) are: overall length 2.22 m; distance from tip of snout to blowhole 16.3, 20, and 20 cm, from tip of snout to apex of flippers 78.5, 87, and 86 cm; length of base of dorsal fin 34, 33, and 42 cm; height of dorsal fin 13, 11, and 17.5 cm; and distance from caudal notch to anal opening 68.5, 82, and 82 cm.

The weight of the animals varies from 136 to 272 kg.

The condylobasal length of the skull is 262–302 mm. The mandibular symphysis is short, 37–46 mm, and smooth on the ventral surface. The alae of the pterygoids and basioccipitals are short. The foramen magnum lies considerably below midskull height.

The skull measurements of a male and two females from Japan (Yamada, 1954) are (in mm): condylobasal length 271, 284, and 297; length of rostrum 140, 165, and 160; width of rostrum at base 128, 136, and 140; interorbital width 218, 240, and 259; and length of lower jaw 224, 253, and 255. (V.S.)

This species is encountered in the coastal waters of South Africa, southern Australia, India, Sri Lanka, Hawaiian Islands, Japan, and off the east coast of the USA. It is known predominantly from beached
627 animals. The maximum number of beached animals has been found on the coasts of Japan and on the eastern coasts of the USA (Handley, 1966).

Geographic variation has not been established.

Biology has not been studied. Differences between the dwarf sperm whale and Owen's dwarf sperm whale are not widely recognized and hence some data on the biology ascribed to *Kogia breviceps* may actually pertain to *Kogia simus*. (V.A.)

Family of Beaked Whales

Family ZIPHIIDAE Gray, 1865⁶

Body dimensions medium and large. Males are larger than females or vice versa.

The body is more or less spindle-shaped. Anteriorly, the snout forms a narrow "beak" sharply demarcated from the frontal adipose body among bottlenose and beaked whales or gradually rising above the head in the rest of the members of the family. The blowhole is crescent-shaped and its bulge may face the head or the tail. The small dorsal fin is situated at the level of the anal opening or slightly anterior to it. There is no notch

⁶ Hyperoodontidae, according to some authors.

between the caudal flukes or it is very small. The flippers are low. The body is usually monochromatic brown or gray but somewhat lighter on the ventral side.

The rostrum is long and narrow, longer than the cranium, with an open mesorostral groove (closed in old animals). The maxillae, premaxillae, and frontal bones bear crests. The palatine bones form part of the anterior wall of the nasal passage. The petrosal bones are fused with the skull. The lachrymal bones are large and not fused with the zygomatic bone. The pterygoids are large and separated by some distance. The lower jaw is wider than the upper and projects forward slightly.

Numerous teeth are seen in the embryos, which reduce in number subsequently. The adults of most of these species have just a few teeth only in the lower jaw. The number of functional teeth varies from $\frac{19}{26}$ in *Tasmacetus* to $\frac{0}{2}$ in *Berardius* and $\frac{0}{1}$ in the rest of the genera.

The number of vertebrae does not exceed 50 and from 2-7 cervical vertebrae are fused. Ribs do not exceed 10 pairs and their sternal sections are not ossified.

The system of air sacs is simple, without preorbital and postorbital lobes. In adult animals, rudiments of the olfactory nerves are preserved. The stomach comprises 4-14 chambers. The members of this family feed mainly on cephalopods (teuthophagous) but also consume fish. They are capable of diving deep and remaining submerged for a long time. Some perform annual migrations. They live singly or in herds, usually comprising 10-15 animals.

These animals are distributed in the warm, temperate, and cold waters of the World Ocean (Fig. 362).

The oldest of the Ziphiidae is evidently *Notocetus* Moreno from the Lower Miocene of Patagonia, resembling in many features the Miocene *Squalodon* Grateloup (family Squalodontidae Brandt) and having, in particular, numerous teeth. Reduction of teeth among the primitive Ziphiidae occurred in the Miocene and typical members of contemporary beaked whales appeared at the end of this period.

The family consists of 17 genera, of which 5 are extant: *Tasmacetus* Oliver (Tasmanian beaked whales), *Berardius* Duvernoy (Pacific beaked whales), *Mesoplodon* Gervais ("sword-tooth dolphins"), *Ziphius* G. Cuvier (Cuvier's beaked whales), and *Hyperoodon* Lacépède (bottlenose whales).

629 The generic division of the family has given rise to no doubts among researchers. However, the systematics of the species of beaked whales requires further development (especially of genus *Mesoplodon*). About 15 species are usually recognized in the family.

Beaked whales are of little economic importance.

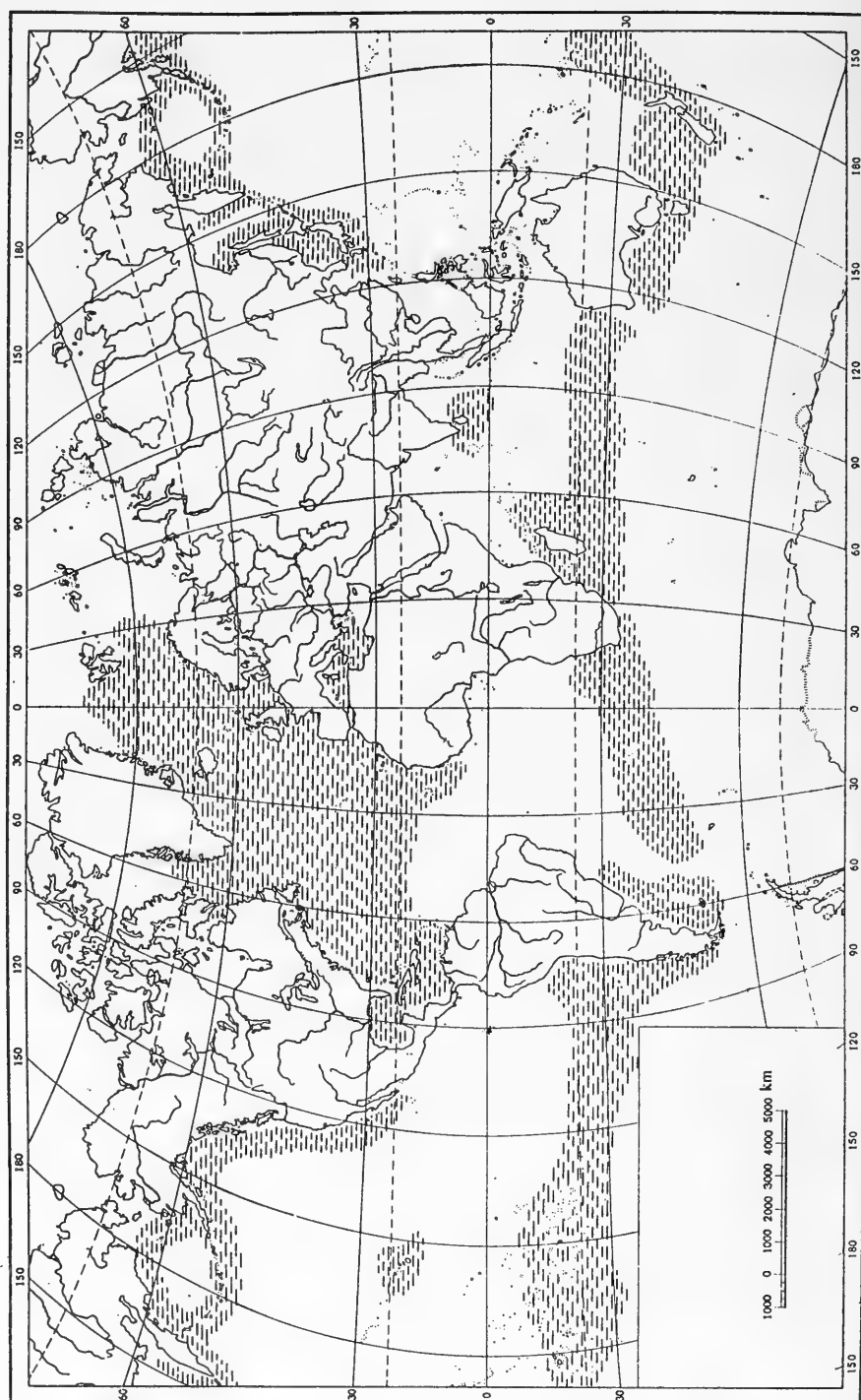


Fig. 362. Range of the family of beaked whales, Ziphiidae (V.A. Arsen'ev).

All of the genera, except *Tasmacetus*, are encountered or could be encountered in USSR waters. Our hunting of these animals is in small numbers. (V.S.)

Genus of Pacific Beaked Whales

Genus *Berardius* Duvernoy, 1851

1851. *Berardius*. Duvernoy. Ann. Sc. Nat., Zoologie, 15, p. 52. *Berardius arnouxii* Duvernoy.

Dimensions large, the largest in the family.

The frontal projection is quite high. The "beak" is highly elongated and somewhat flattened. The low dorsal fin is situated above the anal opening and is not flexed along the posterior margin [falcate]. The flippers are relatively short. The lower jaw is slightly longer than the upper one.

The color is dark brown, the under varying from grey to whitish.

Asymmetry of the skull bones is less manifest than among the other members of the family Ziphiidae. The rostrum is narrow, its length more than double that of the cranium, and it is slightly flattened dorsoventrally. The maxillary crests are low. The premaxillae are symmetrical and their width almost equal throughout their length. The suture between the premaxillae and maxillae does not extend beyond 20% of its length on the dorsolateral surface of the rostrum. The frontal bones have broad orbital processes. The large, massive, rounded, and almost identically sized nasal bones project markedly into the frontals and occupy the highest position on the skull. The mesethmoid bone is only partly ossified.

The anterior section of the lower jaw has two pairs of teeth, of which the anterior larger ones are located at the tip of the lower jaw and remain exposed even when the mouth is closed. The posterior pair of teeth emerge 10-20 cm behind the anterior ones. A few more teeth may remain concealed in the gums.

Cervical vertebrae 7, thoracic 10-11, lumbar 12, and caudal 17-19; total 46-49. The three anterior cervical vertebrae are fused. The sternum consists of five sections.

Biology has not been well studied. These animals remain confined in groups of roughly 20. They feed mainly on cephalopods. Mating and parturition are protracted. Gestation continues for 10 months.

These animals are encountered in the Pacific and Indian oceans and in the South Atlantic.

The genus consists of two species: Arnoux's beaked whale (southern beaked whale), *Berardius arnouxii* Duvernoy, 1851, and Baird's beaked whale (northern beaked whale), *Berardius bairdi* Stejneger, 1883.

Only Baird's beaked whale is encountered in USSR waters.⁷

There is no special hunting for Baird's beaked whale; it is caught only incidentally. (V.S.)

BAIRD'S BEAKED WHALE⁸

Berardius bairdii Stejneger, 1883

1883. *Berardius bairdii*. Stejneger. Proc. U. S. Nat. Mus., 6, p. 77. Staraya Gavan', east coast of Bering Island.
 1883. *Berardius vegae*. Malm. Bihang Svenska Vet. Acad. Handl. 8 (4), p. 109. Commander Islands.
 1947. *Rostrifer nestorésmirnovi*. Zenkovitsh (Zenkovich). Zh. "Rybnoe Khozyaistvo," No. 10, p. 15. Nomen nudum.
 1955. *Berardius vegana*. Bourdelle and Grassé. Traité de Zool., 17, p. 429. Erroneously for *vegae* Malm. (V.H.)

Diagnosis

Only species of the genus found in waters of the USSR.

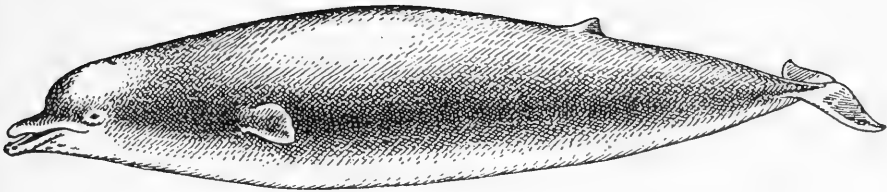
Description

The head is relatively small (Fig. 363). The "beak" is flattened dorsoventrally. The "forehead" of males rises steeply upward and is set off from the "beak" by a distinct transverse groove (Fig. 364). In females the forehead rises more gently and the transverse groove is absent. The blowhole is crescent-shaped and its bulge faces forward. Two (less often, three or four) deep longitudinal grooves occur on the throat (distinctly visible even in embryos; Fig. 364). The shape of the dorsal fin is variable—from low humplike to relatively high and well-proportioned. It is two or three times longer than its height. The flippers are placed close to the ventral surface of the body. They are quite short and broad (length only 2.5–3.2 times their width). The caudal flukes have a small notch.

The body color turns dark with age. In young animals the upper portion is gray with a brown tinge and the abdomen and flanks somewhat

⁷ Baird's beaked whale, caught by our whalers in the Far East, was long erroneously classified as a bottlenose whale (*Hyperoodon*). Only after 1950 (Tomilin, 1952, 1957) was it demonstrated that these animals were actually Baird's beaked whales. Thus all the information about bottlenose whales in the Pacific Ocean reported until 1956 pertains to this species.

⁸ Sometimes, especially in the earlier literature, and also in foreign publications (Hershkovitz, 1966), also referred to as the "Pacific beaked whale". (V.H.)



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Fig. 363. Baird's beaked whale, *Berardius bairdi* (figure by N.N. Kondakov).

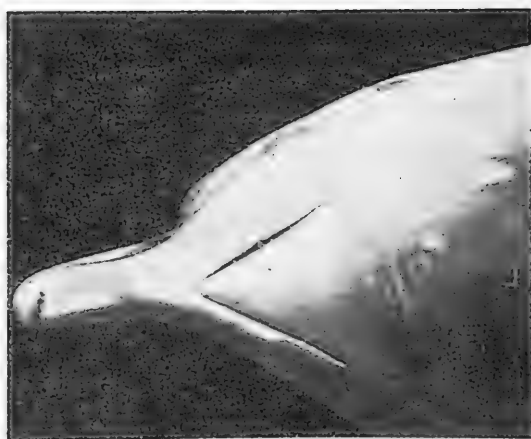


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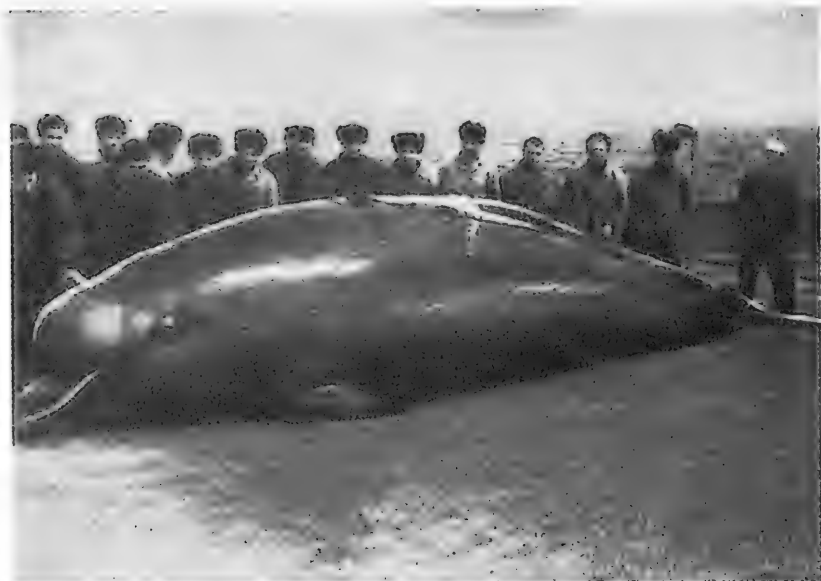
Fig. 364. Head of Baird's beaked whale, *Berardius bairdi*, front view. Pacific Ocean (photograph by M.M. Sleptsov).

lighter. In adult animals the dorsum and flanks are dark brown and the abdomen slightly lighter in color (sometimes may be white). White spots are seen on the skin surface of adult whales in the navel region between the flippers and under the throat. It is possible that these spots reflect an age-related variation of skin pigmentation (Tomilin, 1957). White scars (probably caused by bites of males) are more numerous on the dorsum than on the abdomen. Both the pairs of teeth occur in the region of the mandibular symphysis. The anterior teeth are set on the very tip of the jaw and may rise to a height of 79-89 mm and the posterior ones to 53-67 mm (Omura *et al.*, 1955; Tomilin, 1957). Rear teeth are usually absent in females. In the newborn and suckling calves the teeth are not erupted. In young animals the anterior teeth are conical and may be longer than in adults. With advancing age, the teeth wear down somewhat and become more massive and flattened laterally, especially that part in the alveolus. Barnacles of the genus *Conchoderma* sometimes colonize on the anterior teeth.

631



631 Fig. 365. Head of Baird's beaked whale, *Berardius bairdi*, ventral view. Pacific Ocean (photograph by M.M. Sleptsov).

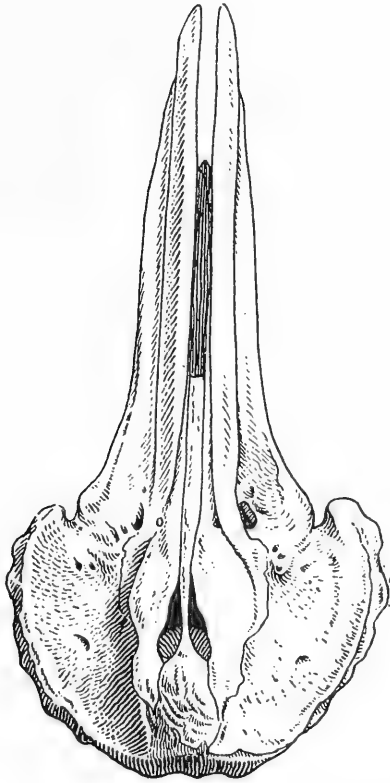


632 Fig. 366. Baird's beaked whale on a deck. Pacific Ocean (photograph by M.M. Sleptsov).

The main measurements of four adult females (Tomilin, 1957) are (in cm): body length 1,225, 1,080, 1,095, and 1,090; distance from tip of upper jaw to blowhole 132, 120, —, and —; distance from anal opening

to posterior edge of caudal flukes 355, —, 323, and 324; length of flippers 152, 108, 118, and 125; height of dorsal fin 30, 30, 31, and 33; and width of caudal flukes (between apices of lobes) 310, —, 270, and 268. The dimensions of males are less than those of females. The maximum known length of a female is 12.2 m, of a male 11.9 m.

The measurements of the skull (Fig. 367) of two adult females and a young male Baird's beaked whale (*Omura et al.*, 1955 and Tomilin, 1957) are respectively (in cm): condylobasal length 152, 142, and 106 (tip of rostrum broken in the male); zygomatic width 75 (measurement not taken in the second female and male); length of rostrum 96, 92, and 52; width of rostrum at base 47, 43, and 31; length of lower jaw 133, 130, and 90; and length of mandibular symphysis 29, 27, and 17. (V.S.)



632 Fig. 367. Skull of Baird's beaked whale, *Berardius bairdi* (figure by N.N. Kondakov).

Geographic Distribution⁹

These animals are distributed in the North Pacific Ocean.

Geographic Range in the USSR (Fig. 368)

In the Sea of Japan, it is distributed in Peter the Great Gulf and along the southern coasts of Sakhalin; in the Sea of Okhotsk, along the islands of the Kuril range and the coasts of western Kamchatka, close to the eastern coasts of Sakhalin, in the Gulf of Sakhalin in waters of the Shantarsk Islands and Iona Island, in the central part of the Sea of Okhotsk; in
 632 the Pacific Ocean, in waters of the Kuril Islands, along the southeastern coast of Kamchatka, in Avachinsk Bay and Kronotskiy Gulf, and around the Commander Islands; and in the Bering Sea, around Karagin Island and in Olyutorskiy Gulf. It apparently does not penetrate farther north than Cape Navarin (about 62° N lat.).

Geographic Range outside the USSR (Fig. 369)

The southern boundary of distribution probably traverses at the latitude of southern Japan. It is known in the Sea of Japan as well as the Pacific Ocean side of the islands of Japan but is more common and abundant in the Pacific Ocean than in the Sea of Japan. On the eastern side of the North Pacific Ocean, it lives from the coasts of California along the entire North American continent to the coasts of the Alaskan peninsula and Aleutian Islands. In the Bering Sea, it is distributed from Bristol Bay and the Pribilof Islands along the boundary of the eastern Bering Sea shallow-water zone to northwest of Cape Navarin on the Asian coast and the southern part of the Gulf of Anadyr (Zenkovich, 1939; Sleptsov, 1955; Tomilin, 1957; Chapskii, 1963). (V.A.)

Geographic Variation

Geographic variation has not been established. It is possible that Baird's and Arnoux's beaked whales (*bairdi* and *arnouxi*) represent only subspecific forms of the same species (Hershkovitz, 1966). Further, there is
 633 justification to assume that the species forms only some local herds or populations and not subspecies. For example, the Pacific Ocean coasts of Honshu and the Sea of Okhotsk's coast of Hokkaido are evidently inhabited by various populations of Pacific beaked whales (Omura, Fujino, and Kimura, 1955; see below). (V.A.)

⁹ [See footnotes on page 854][sic; pp. 843-844—Gen. Ed.]

Biology

Population. Only a few hundred beaked whales are caught every year in the North Pacific Ocean. It may be concluded from this that the population of these whales is comparatively small. However, in most parts of the range the beaked whale is caught only incidentally while hunting for other whales. This no doubt has a bearing on their overall catch.

Food. Data on the food of beaked whales are very meagre. Evidently cephalopods and to a lesser extent fish represent the main food.

Food Objects of Baird's Beaked Whale (Betesheva, 1960, 1961)

Cephalopods

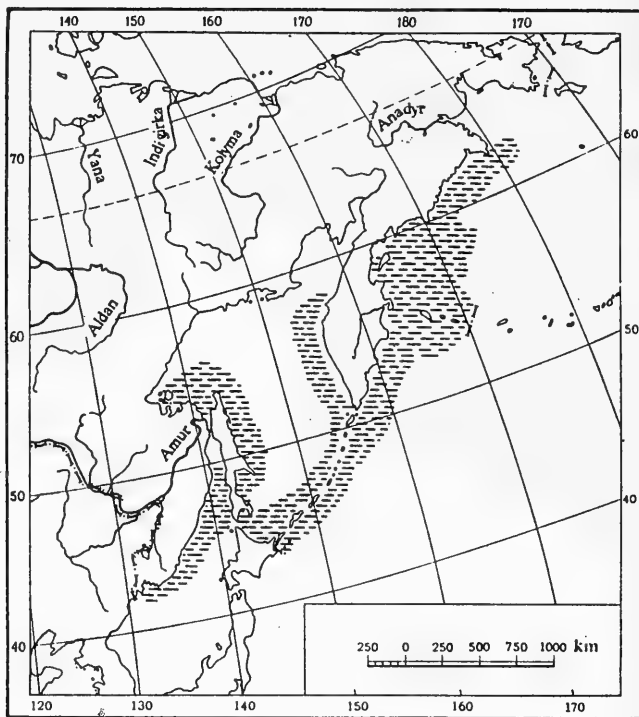
Gonatus magister
Gonatus fabricii
Gonatus borealis
Ommatostrephes sloani-
pacifius

Fish

Alaska pollock, *Theragra*
chalcogramma
Podonema, Podonema longipes
Navaga, Eleginus navaga
gracilis
 Albatross rat-tail, *Coryphaenoides*
pectoralis
 Black rat-tail, *Hemimacrus*
acrolepis = [*Coryphaenoides*
acrolepis]

There are references to finds of redfish (ocean perch), skates and their eggs in the stomach of beaked whales (Zenkovich, 1939; Tomilin, 1957).

635 *Daily activity and behavior.* Pacific beaked whales are usually confined to groups of 5-7 each or sometimes up to 20 animals (Zenkovich, 1939). They dive for 8-20 min (less frequently up to one hour) after which they "rest" on the sea surface for 3-4 min producing 10-15 blows in this period. The blow of the beaked whale is low, 1.0-1.5 m in height (Tomilin, 1957). On surfacing after prolonged submergence, the forehead of the whale is seen first on the surface followed immediately by a small blow. The anterior part of the dorsum and the dorsal fin are seen next. During intermediate submergences, only the upper end of the dorsal fin is exposed since the whale floats right on the water surface almost without flexing the body. Before undertaking a fresh prolonged submergence, at the moment of appearance of the dorsal fin, the body flexes and the head is concealed under water. Next the anterior part of the trunk is gradually flexed more sharply and assumes an almost vertical posture. The dorsal fin and the caudal stem adjoining it then gradually rise above the water and, when they are highest above the surface, the entire body



633 Fig. 368. Range of Baird's beaked whale, *Berardius bairdi*, in the USSR (V.A. Arsen'ev).

begins to descend slowly and that part of the trunk visible above the water gradually submerges into the sea, the last to disappear being the caudal flukes. However, the caudal flukes, unlike in sperm whales, do not rise out of the water.

On surfacing, the beaked whales form a typical chain, sometimes in twos or even threes, one behind the other (Fig. 370). The animals leap from the water at an angle to the sea surface roughly equal to one-third the length of the trunk, then fall on the water with a loud thud (Tomilin, 1957). Sometimes they completely breach the water and dive with the head down like a dolphin without landing on the flanks or on the abdomen, as generally happens in the case of large whales.

The herds usually differ in composition. Adult males and females with calves remain singly, far away from the coasts, forming independent herds, while young animals gather in separate groups close to the coasts and transgress even into bays and gulfs (Zenkovich, 1939). Mixed herds are also noticed, with males, females, and young animals living together

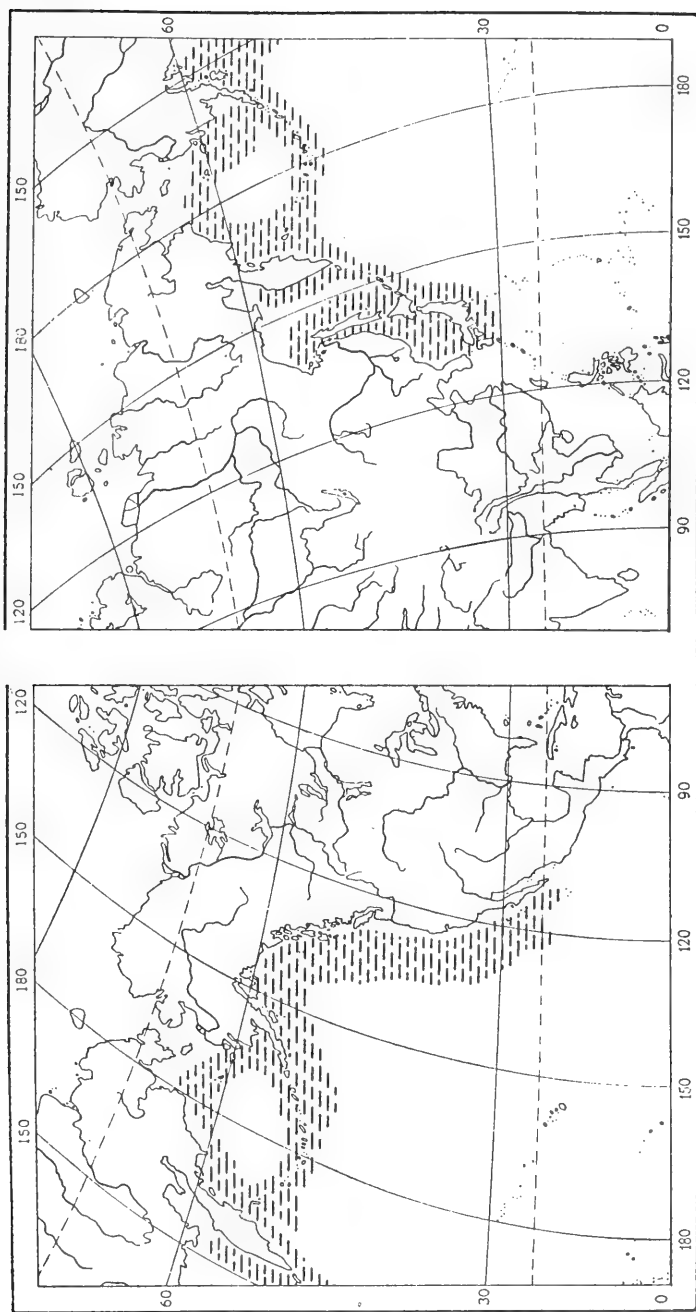
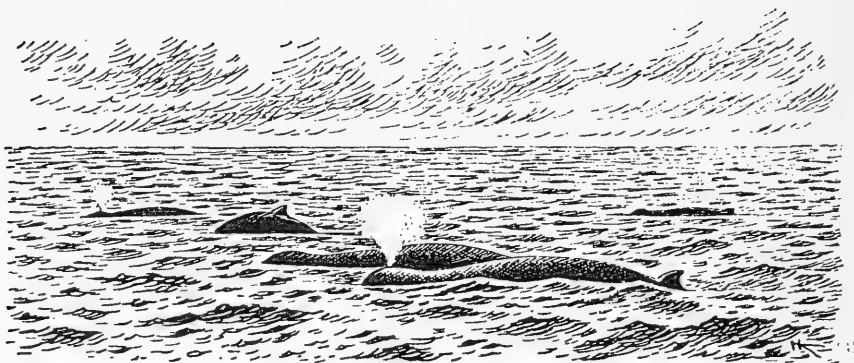


Fig. 369. Species range of Baird's beaked whale, *Berardius bairdi* (V.A. Arsen'ev).



635 Fig. 370. Baird's beaked whale, *Berardius bairdi*, at sea (figure by N.N. Kondakov).

(Tomilin, 1962). Many cases of beached Baird's beaked whales have been recorded: near Centerville and Santa Cruz on the Californian coast, in Tokyo Bay in Japan, and on the Pribilof and Commander Islands.

Seasonal migrations and transgressions. Beaked whales perform regular seasonal migrations but their periods and courses have not been established. It is known that they appear in spring in the northern part of the range, in the Sea of Okhotsk and the Bering Sea, and leave for the south in autumn for the waters of California and southern Japan
636 where they winter. Since more beaked whales are caught along the Pacific Ocean coast of Honshu than in the Sea of Japan, it has been assumed that most of the herd wintering in southern Japan migrates north along the eastern side of the islands of Japan. Here they are seen in early May with the maximum number sighted in the waters of Japan in July and August, fewer in September, and hunting ceases altogether in November. Apparently a part of this herd (population) spends the summer months in the waters of Japan and another part farther north since, in May, June, and July, they are noticed along the eastern coast of Kamchatka and in August near the Commander Islands, Karagin Island, and in Olyutorskiy Gulf (Zenkovich, 1939).

In the Sea of Japan, beaked whales are seen earlier than along the coasts of the more southward Honshu Island. In March they are sighted in Peter the Great Gulf and in April, along the northeastern coasts of Hokkaido in the Sea of Okhotsk. In May the hunting of beaked whales in Hokkaido increases considerably, lessens in June, and ceases almost altogether by July and August. In September and October the second arrival of beaked whales occurs off the Hokkaido coasts and their catch in these months increases again. It is possible that an independent population of

beaked whales lives here, migrating in summer into the Sea of Okhotsk and again appearing in autumn during autumn migrations to the wintering sites.

A preponderance of males has been recorded in the annual catch of beaked whales from the coastal stations in the waters of Japan. In five years of hunting, they totaled 68.3% of the total catch. It would seem that whales of different sex (and probably of age) groups migrate at different periods by different routes (Omura, Fujino, and Kimura, 1955).

Reproduction. Mating and parturition occur in winter months in the wintering areas, but have not been established very accurately. The majority mate in February with most births recorded in December. Both these periods are perhaps protracted by a few months. On August 5, 1957, a female 1,076 cm long held an embryo 12 cm long. Apparently this female had mated in summer. On the other hand, on August 21, 1927, a female caught in the same region was found with an embryo 242 cm long. This female had perhaps mated in winter. Gestation extends for about 10 months (Omura, Fujino, and Kimura, 1955; Omura, 1958).

Growth and development. Adults and embryos differ in body proportions (Omura, Fujino, and Kimura, 1955). Among embryos: (1) the head is relatively large; (2) flippers are shifted closer to the tail; (3) flippers are relatively large; (4) navel caudally situated although position of the anal opening is the same as in adults; (5) dorsal fin is relatively very high although its relative length along the base is the same as in adults; and (6) caudal flukes at the point of their articulation with the caudal stem are relatively broader. The average size of newborn calves is 4.6 m. Calves 580 cm long were still suckling.

The animals attain sexual maturity at three years of age or slightly later at an average body length of 10.1 - 10.4 m (females) and 9.7 - 10.1 m (males) (Table 63).

The smallest pregnant female was 9.8 m long and the largest immature female 10.4 m (Tomilin, 1962).

Enemies, diseases, mortality, parasites, and competitors. It would appear that Pacific beaked whales have no enemies. Their diseases have not been studied. From among the ectoparasites, whale lice of the genus *Platycyamus* have been found. Some instances of barnacles (*Conchoderma*) adhering to the teeth have also been recorded. Overgrowth of diatomaceous algae *Cockoneis* sp. and *Navicula* sp. and adhesions caused by suction of the Pacific lamprey (*Entosphenus tridentatus*) have also been observed.

Nine species of endoparasites are known: trematodes one, cestodes two, nematodes four, and acanthocephalans two. The trematode *Oschmarinella sobolevi* Skrjabin has been detected in the bile ducts of the

637 Table 63. Dimensions of Pacific beaked whales caught in the waters of Japan (Omura, Fujino, and Kimura, 1955)

Length of whale, m	Caught		Total
	Males	Females	
5.5	—	1	1
5.8	—	1	1
6.1	—	1	1
7.0	2	3	5
7.3	1	4	5
7.6	1	1	2
7.9	1	—	1
8.2	6	2	8
8.5	4	4	8
8.8	8	6	14
9.1	25	17	42
9.4	19	11	30
9.7	38	17	55
10.1	76	18	94
10.4	149	38	187
10.7	158	50	208
11.0	91	61	152
11.3	43	33	76
11.6	9	20	29
11.9	—	4	4
12.2	—	1	1

liver in beaked whales only from Kuril waters. Neither of the cestodes
637 *Trigonocotyle* sp. and Tetrarhynchidae gen. sp. has been identified at the species level. Of the four species of nematodes found in beaked whales, *Anisakis* (*Anisakis*) *simplex* Rudolphi, parasitizing the gullet, stomach, and intestine, is very widely distributed among marine mammals. It is known among many species of toothed and baleen whales and Steller's sea lion among Pinnipedia (detected in the North Sea, off the coasts of Kamchatka, Japan, and New Zealand). The nematode *Anisakis skrjabini* Mosgovoy, found in beaked whales and sperm whales in the waters of the Commander Islands, the Sea of Okhotsk, and in the Antarctica, localizes in the stomach and small intestine. *Crassicauda giliakiana* Skrjabin and Andreeva has been found in the kidneys and ureter of beaked whales and belugas of the Sea of Okhotsk and *Delamurella hyperoodoni* Gubanov in the lungs (tracheae) of only the beaked whale of the Sea of Okhotsk. The acanthocephalan *Bolbosoma nipponicum* Yamaguti detected in the intestine of beaked whales from Kuril waters is also known among three species of baleen whales and two species of pinnipeds of the Kuril Islands and the seas of Japan and Okhotsk. *Echinorhynchus gadi*, detected in the

stomach of beaked whales, is a known parasite of fish (Delamure, 1955; A. Skrjabin, 1959, 1960).

The extent of mortality among beaked whales is not known. These whales face some competition for food from sperm whales.

Field characteristics. The body length is around 10 m (for adults) and the color monochromatic—dark brown on top and lighter below. The “beak” is flattened. The anterior mandibular section has two pairs of teeth. The much larger first pair projects outward with the mouth closed. The dorsal fin is high and well-proportioned and situated above the anal opening. These animals live in small groups, dive simultaneously, and never display the caudal flukes. The blow is small, at a height of 1.0–1.5 m, resembles a flash, and is bushy. (V.A.)

Economic Importance

Minimal but regular hunting of Baird’s beaked whale is carried out only in the waters of Japan. At other places this whale has no economic importance (Table 64).

The Japanese and Soviet whaling fleets catch some ten beaked whales every year while hunting for large whales; the coastal stations of British Columbia and California on the North American coast also catch a few of these whales.

As these whales are of small dimensions, the quantum of products obtained from them is also comparatively small (Table 65).

The quantity of fat obtained from one average size whale is, on average, 2,700 kg (Khar’kov, 1940).

638 Japanese whalers catch beaked whales using small boats equipped with small-bore harpoon guns in the same manner as in hunting large

Table 64. Catch of beaked whales in the waters of Japan (international whaling statistics)

Year	Whales caught	Year	Whales caught
1948	73	1959	186
1949	92	1960	147
1950	186	1961	133
1951	252	1962	145
1952	321	1963	160
1953	262	1964	189
1954	—	1965	172
1955	258	1966	171
1956	297	1967	107
1957	186	1968	117
1958	229		

whales using large whale boats. The animals caught are brought to the coastal stations.

The fat of these whales is used only for commercial purposes. The fat from the jaws (from the mandibular hollow space) and around the jaws serves as raw material for producing a high-quality oil useful for lubricating fine mechanisms. The flesh is generally not used as food but, after cooking, can be used for feeding fur-bearing animals. In some cases, however, the flesh of these whales is processed for human consumption also.

Based on their population, the hunting of beaked whales could be somewhat expanded. Rules for controlling hunting have not been formulated and, at the present rate of their exploitation, there is yet no need for such. (V.A.)

Genus of Beaked Whales [Sword-tooth Dolphins]

Genus *Mesoplodon* Gervais, 1850

1850. *Mesoplodon*. Gervais. Ann. Sc. Nat., Zoologie, 14, p. 16. *Delphinus sowerbiensis* Blainville = *Physeter bidens* Sowerby. (V.H.)

Medium body dimensions, with a length up to 6.7 m.

The dorsal fin is low and its apex flexed posteriorly. The flippers are pointed at the tips. The bulge of the crescent-shaped blowhole faces backward. The sloping forehead transits gradually into a fairly long beak. The body color is dark (from black to gray) and the abdomen light-colored.

The long and thin rostrum is narrower on top than in other members of the family of beaked whales and exhibits mesorostral ossification,

638 Table 65. Weight of body parts of Baird's beaked whales (Zenkovich, 1937b; Tomilin, 1951; Sleptsov, 1961)

Body part	Body length and sex		
	Female 10.0 m	Female 10.8 m	? 11.1 m
Subcutaneous fat	3,337	2,258	5,616
Flesh	2,400	2,838	1,974 ¹
Skeleton	1,953	1,256	3,050 ¹
Viscera	958	1,148	399
Total	8,648	7,500	11,039

Note: The heart, lungs, and liver of another female, 11.1 m long (pregnant), weighed 54, 281, and 64.5 kg respectively (Khar'kov, 1940).

[¹These figures are possibly reversed.—Ed.]

formed through ossification and fusion with the surrounding bones of the vomer. The supraoccipital and interparietal bones form a high crest. The frontal bones have small orbital processes. The mandibular symphysis is considerable in size (one-fifth to one-third the jaw length).

One pair of teeth, strongly compressed laterally, is located at the level of the anterior third of the lower jaw (at the end of the jaw only in *M. mirus*) and projects outside the mouth when it is closed, while covering the upper jaw from the sides. The roots of the teeth run obliquely to the longitudinal axis of the jaw. Among some species of these beaked whales, the teeth are sharply enlarged; they are larger among males than females. Numerous minute teeth are concealed in the gums of the upper and lower jaws, particularly among young animals (they may be resorbed with advancing age).

Cervical vertebrae 7, thoracic 9-11, lumbar 9-12, and caudal 18-21; total 46-48. The atlas and axis are fused; sometimes a third cervical vertebra is attached to them. The spinous vertebral processes are very large. The sternum has four (less often five) sections. Of the five digits on the forelimb, the second and third are the longest.

Biology very poorly studied. These are pelagic whales, rarely encountered along coasts. They remain singly, in small groups, or much larger herds. They apparently feed mainly on cephalopods. The periods of mating and parturition are very prolonged.

The distribution is extremely wide: in the eastern part of the Atlantic Ocean, from Norway and the British Isles to Madeira, the Mediterranean Sea, and coasts of South Africa; in the western Atlantic, from Newfoundland and Canada; and in the Caribbean Sea, from Trinidad and the coast of Argentina (42° S lat.) to the Falkland Islands. In the Pacific Ocean, in the east from the Bering Sea to La Jolla in California in the north and along the coasts of Chile in the south, and in the west from the Bering Sea to Japan and from Australia to New Zealand; and the Indian Ocean (Hershkovitz, 1966). Abundant everywhere (Fig. 371).

Fossil remains have been found in the Upper Miocene of North America and in the Upper Miocene and Middle Pliocene of Europe.

The genus comprises 10 (Nishiwaki and Kamiya, 1958; Hershkovitz, 1966) or 11 (Moore, 1968) species: *M. bidens* Sowerby, 1804—North Atlantic from Norway, the Baltic Sea, and Great Britain in the east to the Mediterranean Sea (inclusive) and in the west from Newfoundland to Massachusetts state (USA); *M. europaeus* Gervais, 1848-1852—North Atlantic (English Channel and from New York to Florida, Gulf of Mexico, and also the Caribbean Sea from Cuba to Trinidad); *M. mirus* True, 1913—North Atlantic (British Isles and coasts of France and from Cape Breton and Nova Scotia peninsula to Florida), South Atlantic (southern

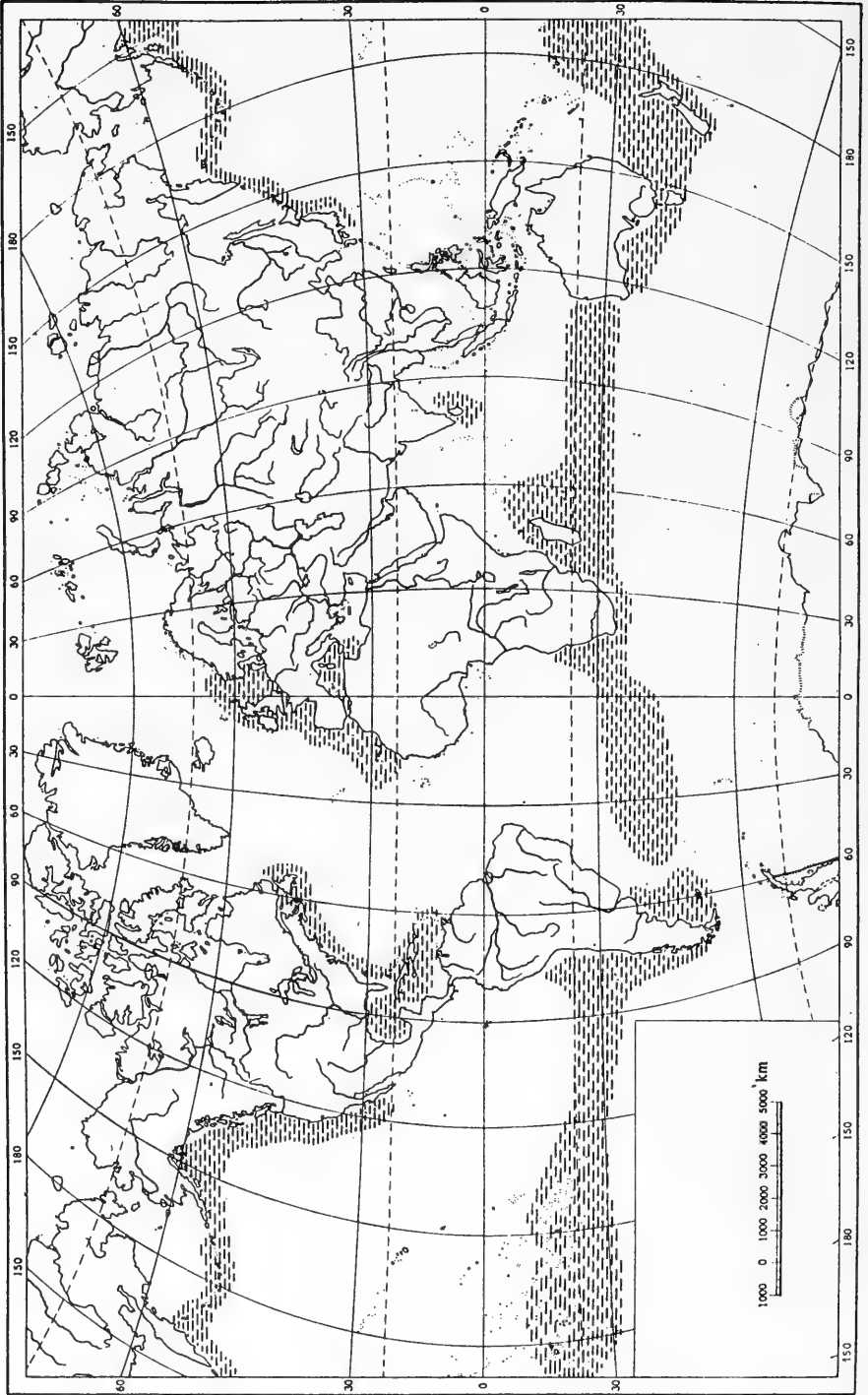


Fig. 371. Range of the genus of beaked whales [sword-tooth dolphins], *Mesoplodon* (V.A. Arsen'ev).

641 coasts of South Africa); *M. grayi* Haast, 1874—Indian Ocean (coasts of South Africa and Australia), South Pacific Ocean (from New Zealand to Chilean coasts), South Atlantic from the coasts of Argentina and the Falkland Islands to South Africa, North Atlantic (Netherlands coast); *M. ginkgodens* Nishiwaki and Kamiya, 1958—North Pacific Ocean from Japan in the west to California in the east and coasts of Sri Lanka in the Indian Ocean; *M. layardi* Gray, 1865—South Pacific Ocean and Indian Ocean from Australia and New Zealand to the South Atlantic between the Falkland Islands and South Africa; *M. densirostris* Blainville, 1817—eastern part of the Atlantic Ocean (coastal waters of Madeira and South Africa), western Atlantic (Nova Scotia peninsula, Canada, and Bahama Islands), western part of the Pacific Ocean (Lord Howe Island and Queensland in Australia), North Pacific Ocean (Midway Island), and Indian Ocean (from South Africa and the Seychelles to apparently western Australia); *M. stejnegeri* True, 1885—Pacific Ocean from the Bering Sea to Oregon state (USA) in the east and Japan in the west; *M. bowdoini* Andrews, 1908—New Zealand coast; *M. carlhubbsi* Moore, 1946 [1963]—North Pacific Ocean (east coast of Japan and west coast of the USA between 32° and 47° N lat.); and *M. hectori* Gray, 1871—Southern hemisphere, temperate waters.

The systematics of the genus of beaked whales has not been sufficiently developed. Many species have been described on the basis of just one or two specimens and the differences between some of them represent only individual variations. Thus, it is possible that *M. stejnegeri*, *M. bowdoini*, *M. ginkgodens*, and *M. carlhubbsi*, inhabiting the Pacific Ocean, belong to the same species, as conceded by some scientists who regard the differences between these species as inconsequential. The main differences are: the lateral thickness of the tooth crown is greater than its front-to-back width—in *M. stejnegeri* by seven times, *M. ginkgodens* six times, and *M. bowdoini* three or four times; and the premaxillary foramina lie at the same level as the maxillary foramina or posterior to it in *M. stejnegeri* and *M. bowdoini*, but markedly more anteriorly in *M. ginkgodens*. There are other differences also. The collection of more factual data should clarify the systematics of the genus.

On the other hand, the differences between some species (groups of species) are quite significant. Thus, *M. layardi* Gray is isolated in a special subgenus, *Dolichodon* Gray, *M. densirostris* Blainville in subgenus *Dioplodon* Gervais, and all the rest of the species placed in the subgenus *Mesoplodon* Gervais (Moore, 1968).

Only one species, Stejneger's beaked whale, *M. stejnegeri*, has been reported in USSR waters. Some other species may also be encountered: in the southern part of the Baltic Sea—Sowerby's beaked whale,

M. bidens; in the seas of the Far East—*M. carlhubbsi* and *M. ginkgodens*. The latter two species could, however, be regarded as belonging to the species *M. stejnegeri* and hence are not described here.

There is no special hunting of these beaked whales. (V.S.)

STEJNEGER'S BEAKED WHALE

Mesoplodon (Mesoplodon) stejnegeri True, 1885

1885. *Mesoplodon stejnegeri*. True. Proc. U.S. Nat. Mus., 8, p. 585. Bering Island and Commander Islands. (V.H.)

Diagnosis

Total body length up to 6 m.

Color black, more light-colored ventrally. The antorbital notches in the skull are developed relatively poorly. The foramina of pair V of the nerves in the maxilla lies anterior to that in the premaxilla or at the same level. The palatine bones are not adjacent. The ratio of length of tooth crown to its width is more than in the other species of these beaked whales (6.4:1 or even slightly more). (V.S.)

Description

The lower jaw is longer than the upper by 15 mm. The flippers are relatively small. The caudal flukes are lighter in color than the trunk and may be white on the underside. Quite a large number of small white patches (traces of scars or parasitic infections) are present on the body surface (Fig. 372). The teeth are strongly built in the males (Fig. 373) but barely emerge from the gums in the females.

642 The following are the main body measurements of an adult male Stejneger's beaked whale (Tomilin, 1957) (in cm): body length 509; maximum girth of body 254; distance from tip of lower jaw to base of flippers 112; distance from tip of upper jaw to anterior margin of blowhole 59; distance from anal opening to notch between the caudal flukes 141;

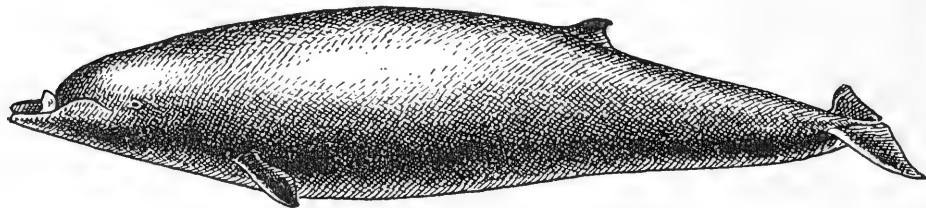


Fig. 372. Stejneger's beaked whale, *Mesoplodon stejnegeri* (figure by N.N. Kondakov).

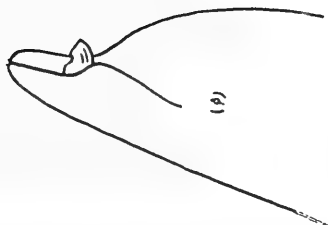


Fig. 373. Head of Stejneger's beaked whale, *Mesoplodon stejnegeri*, lateral view (figure by N.N. Kondakov).

length of flippers along the anterior (lower) margin 55; maximum width of flippers 16; height of dorsal fin 21; length of dorsal fin along the base 34; and spread of caudal flukes 128.

The main measurements of the skull (Fig. 374) of male Stejneger's beaked whales caught off the coasts of Oregon and California (two specimens), and Japan (one specimen) (Tomilin, 1957; Nishiwaki and Kamiya, 1959) are respectively (in cm): condylobasal length 81, 82, and 80; zygomatic width 39, 38, and 38; length of rostrum 49, 51, and 49; width of rostrum at base 23, 22, and 16; length of lower jaw 69, 71, and 68; and length of mandibular symphysis 18,—, and 18. (V.S.)

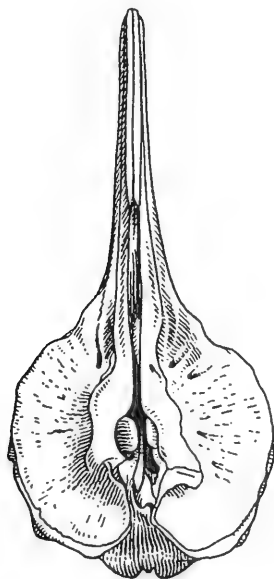


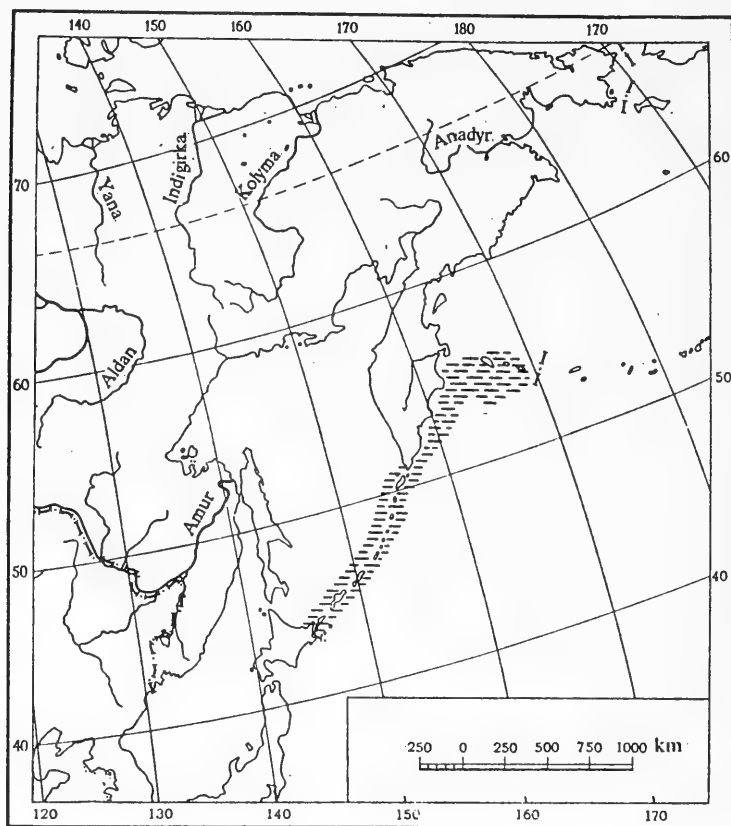
Fig. 374. Skull of Stejneger's beaked whale, *Mesoplodon stejnegeri* (figure by N.N. Kondakov).

Geographic Distribution and Biology

Pacific Ocean from the Bering Sea to the Californian coast in the east and coasts of Japan in the west (information on distribution is based exclusively on the sites of animals stranded on coasts; field observations are almost nil).

Geographic Range in the USSR (Fig. 375)

Known only from the waters of the Commander Islands where three instances of beached beaked whales have been recorded on the shores of the Bering Sea. Their presence is possible in the waters of Kamchatka and the Kuril Islands.



Geographic Range outside the USSR (Fig. 376)

Aleutian Islands (one record), Alaskan peninsula (one record), Pacific Ocean coast of North America (five records off the coasts of Washington, Oregon, and California states), and Japanese coasts (two records in the region of Ayukawa) (Tomilin, 1962; Hershkovitz, 1966).

Geographic variation has not been established.

- 643 Biology virtually not studied since the species is very rare throughout its range. Cephalopods apparently serve as the main food although some individual whales have been sighted at the sites of congregations of salmon. The very small number of observations indicate that they live singly or in very small groups (up to three animals). In life style, they are probably similar, if not identical, to Sowerby's beaked whale (*M. bidens* Sowerby, 1804).

Adult animals are about 6 m long and black with a light-colored underside. Teeth one pair, strongly compressed laterally, project from the sides, and cover the upper jaw when the mouth is closed.

These whales are of almost no economic importance. (V.A.)

SOWERBY'S BEAKED WHALE

Mesoplodon (Mesoplodon) bidens Sowerby, 1804

1804. *Physeter bidens*. Sowerby. Trans. Linn. Soc. London, 7, p. 310. Elginshire, Scotland.
1817. *Delphinus sowerbensis*. Blainville. Nouv. Dict. Hist. Nat. 9, p. 177. Substituted for *Physeter bidens* Sowerby. (V.H.)

Diagnosis

Maximum overall body length up to 5.5 m.

Body dorsally black or bluish-black and usually grayish or whitish ventrally. The antorbital notches are well developed in the skull. The foramina of pair V of the nerves in the maxilla is located posterior to the foramina in the premaxilla. The palatine bones are adjacent. The rostrum is broad at the base. The teeth lie posterior to the mandibular symphysis. The ratio of length of tooth crown to its width is 3.5:1. (V.S.)

Description

The head is slightly compressed laterally. The "beak" is slightly flattened dorsoventrally (Figs. 377 and 378). The lower jaw is only

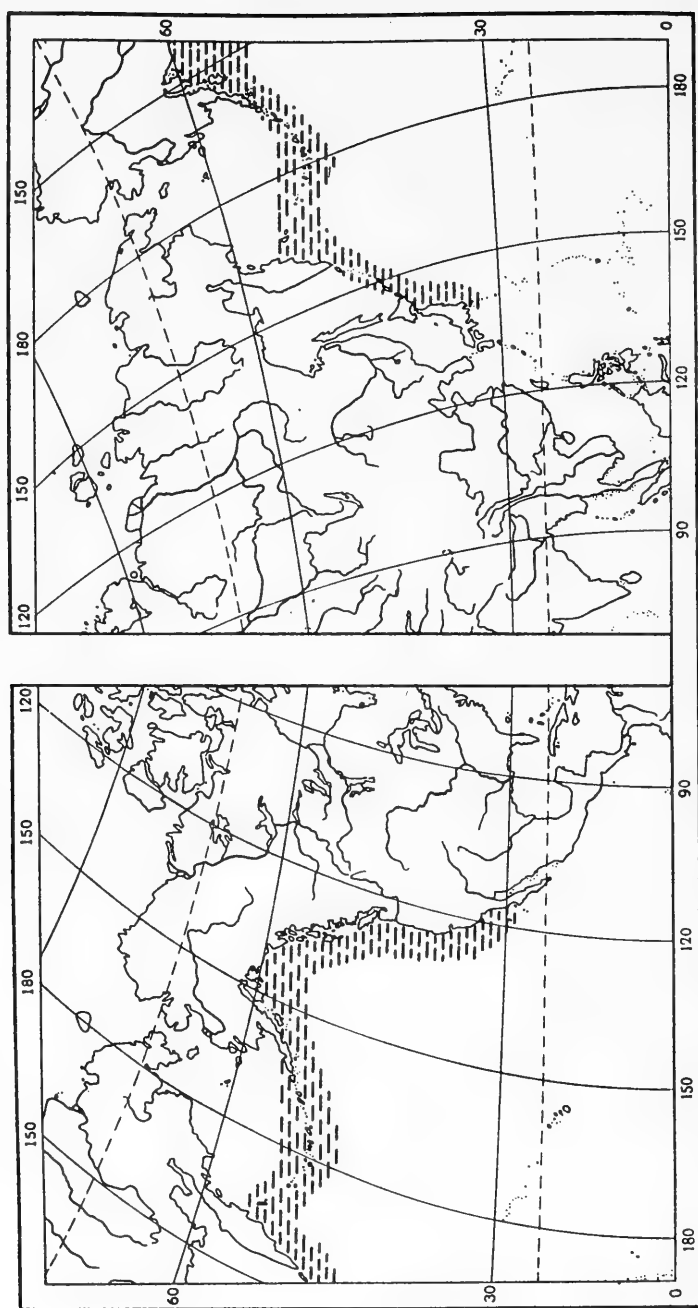
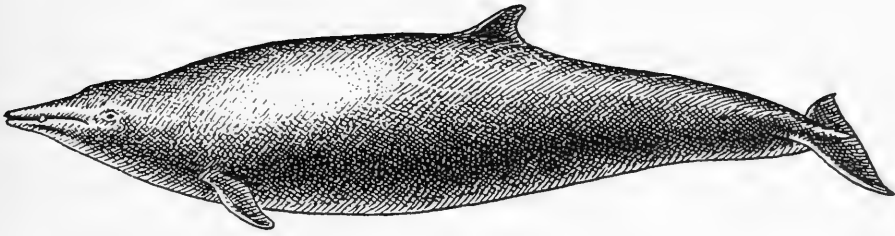
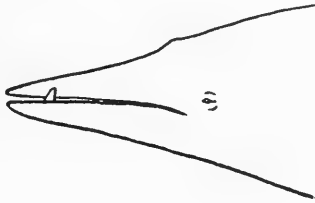


Fig. 376. Species range of Stejneger's beaked whale, *Mesoplodon stejnegeri* (V.A. Arsen'ev).



645 Fig. 377. Sowerby's beaked whale, *Mesoplodon bidens* (figure by N.N. Kondakov).



645 Fig. 378. Head of Sowerby's beaked whale, *Mesoplodon bidens* (figure by N.N. Kondakov).

insignificantly longer than the upper (roughly by 13 mm). The body color is variable—from black to gray with abdomen light, sometimes white. The anterior margin of the caudal flukes and the upper and lower jaws may be light-colored. Numerous whitish spots and bands—remnants of scars—cover the body. The teeth of males are much larger than in females; in the latter, the teeth in most cases do not emerge from the gums.

The basic body measurements of two female Sowerby's beaked whales are as follows (Tomilin, 1957) (in cm): body length 345 and 431; distance from tip of snout (in second animal from tip of lower jaw) to flippers 91 and 109.8, up to blowhole 44 and —; length of flippers 30 and 39.2, their width 12 and 13; distance from tip of snout to dorsal fin 204 and 275.8; height of dorsal fin 27 and 20.9, its length 49 and 36.6; and spread of caudal flukes 68 and 99.4.

The basic skull measurements (Fig. 379) of three males caught off the Shetland Islands, Norway, and Sweden (Tomilin, 1957) are respectively (in cm): condylobasal length 74, 73, and 74; zygomatic width 29, 30, and 27; length of rostrum —, 48, and 50; width of rostrum at base 18, 19, and 17; length of lower jaw 70, 64, and 64; and length of mandibular symphysis —, 21, and 22. (V.S.)

Geographic Distribution

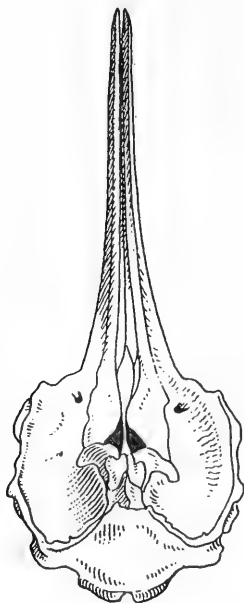
North Atlantic Ocean from the coasts of Norway, the British Isles, and the Baltic Sea up to the Mediterranean Sea in the east and from Newfoundland to Massachusetts state along the American coast (the distribution of the species was established exclusively from information on beached animals).

Geographic Range in the USSR

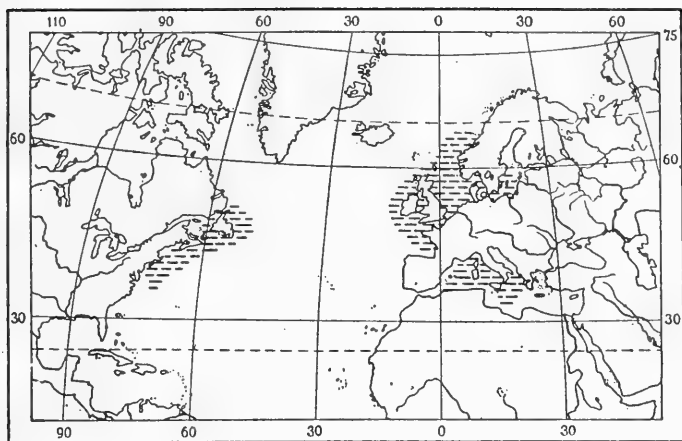
Stray transgressions are possible into our waters in the Baltic Sea.

Geographic Range outside the USSR (Fig. 380)

Finds of beached animals are known in Newfoundland and Massachusetts state on the North American coast. In the eastern part of the North Atlantic, they have been registered on the coasts of Norway, Sweden, England, Poland, Holland, the FRG, the GDR, Belgium, and France. This whale is encountered in the Mediterranean Sea (Sergeant and Fisher, 1957). (V.A.)



645 · Fig. 379. Skullof Sowerby's beaked whale, *Mesoplodon bidens* (figure by N.N. Kondakov).



646 Fig. 380. Species range of Sowerby's beaked whale, *Mesoplodon bidens* (V.A. Arsen'ev).

Geographic Variation

Not established.

646

Biology

Very poorly studied. Absolutely nothing is known about the population of Sowerby's beaked whales. Information on their food is not available.

Behavior. These whales are seen more often singly or in pairs. In the shallow-water bays of Khërtvik on Gassen Island (Norway), the "technique" of two of these whales stranded on the coast was observed on April 18, 1957. Initially, they swam along the coast to a shallow point almost touching the bottom. For a quarter of an hour they attempted to return to the sea but a low tide occurred and the exit from the bay became very shallow. Then, the larger of the two whales turned directly toward the coast and soon found itself on a sandy beach. It quivered its tail vigorously and within minutes a large pit had formed in the sand. Meanwhile the smaller whale swam along the coast but having covered a distance of only 20 m slammed against some rocks and remained motionless; it resisted only slightly when its tail was looped. From the first sighting of these animals along the coast to their death, no more than 30 min elapsed. One was an adult female 505 cm in body length and the other a large female calf 315 cm long (Jonsgard and Hoidal, 1957).

Seasonal migrations and transgressions. In La Mancha Strait and on the coasts of Great Britain, beached Sowerby's beaked whales have been found in March, April, September, and December; in the Baltic Sea,

such finds have been recorded in February, June, August, and September. These animals are believed to inhabit these waters throughout the year. Their migrations have not been traced.

Reproduction, growth, and development. Mating and parturition occur at the end of winter and spring. The period of mating is quite prolonged. Gestation extends for about a year. The body length of a calf at birth varies from 152 to 213-244 (\bar{x} 183) cm. In the period of lactation, the calf adds 90-120 cm to its length. Suckling ceases at a body length of about 300 cm (Jonsgard and Hoidal, 1957).

Enemies, diseases, mortality, parasites, and competitors. Enemies of Sowerby's beaked whale are not known. The diseases have not been studied.

An endoparasite (*Conchoderma* sp.) was found on the teeth of Sowerby's beaked whale. Six species of helminths are known. Cysts of the trematode *Monostomum delphini* Diesing were found in the blubber of a whale from Gavra region but the highly superficial description does not permit positive identification of the species affinity of this parasite. The cestode *Strobilocephalus triangularis* Diesing, detected in the intestine of Sowerby's beaked whale, is also known in the bottlenose whale and two or three species of dolphins. It has been found off the coasts of Portugal and Brazil. The cestode *Tetrabotheum forsteri* Krefft, parasitizing the intestine of Sowerby's beaked whale, was also detected in two species of dolphins from the Mediterranean Sea and New Zealand waters. The widely distributed cestode *Phyllobothrium delphini* Bosk, parasitizing the skin of Sowerby's beaked whale, is also known in seven species of toothed whales, the Arctic whale, and Weddell's seal. It has been detected near the Azores, in the Mediterranean Sea, off the Commander Islands, along the coasts of Australia, and in the Antarctic.

The nematode *Anisakis (Anisakis) simplex* Rudolphi is very widely distributed and, in addition to Sowerby's beaked whale, parasitizes the gullet, stomach, and intestine of ten other species of toothed whales, two species of baleen whales, and Steller's sea lion. It has been detected in the North Sea and off the coasts of Kamchatka, Japan, and New Zealand. The only species of acanthocephalans, *Bolbosoma vasculosum* Rudolphi, was found in the intestine of Sowerby's beaked whale and the common dolphin from the Atlantic Ocean and the Mediterranean Sea (Delamure, 1955).

647 *Field characteristics.* The maximum body length is 5.5 m. The body is almost black dorsally and slightly lighter ventrally. The lower jaw is almost not longer than the upper. The teeth almost do not emerge among females. With the mouth closed, a pair of large flat teeth projects upward along the sides of the upper jaw in males.

Sowerby's beaked whale has no economic importance and there is no hunting of this animal. (V.A.)

Genus of Goose-beak [Cuvier's Beaked] Whales

Genus *Ziphius* G. Cuvier, 1823

1823. *Ziphius*. G. Cuvier. Rech. ossem. foss., 5, p. 350. *Z. cavirostris* G. Cuvier.

1846. *Xiphius*. Agassiz. Nomencl. Zool., p. 389. Correction for *Ziphius* G. Cuvier. (V.H.)

Medium size, with body length up to 8 m.

The "beak" is short and transitions smoothly into the low frontal projection of the corpus adiposum. The jaw line is short. The dorsal fin is low and highly variable in shape in different animals, from crescent-shaped to triangular. The flippers are relatively long and narrow. The lower jaw projects forward more than the upper. The jaw line extends posteriorly to less than half the distance between the tip of the snout and the eye.

The color is usually dark and subject to considerable individual variation. The dorsum may be lighter in color.

The skull is asymmetric. Among the members of the family, the rostrum of the skull is the widest and shortest (only slightly longer than the cranium) in this genus. The vomer forms a stable mesorostral ossification. Longitudinal maxillary crests are very poorly developed. A large depression, housing the spermaceti sac, occurs on the dorsal side of the skull between the outer edges of the maxillae. The mesethmoid bone is ossified. Posterior to the nostrils, the maxillary, premaxillary, and nasal bones form a large projection in the form of an arch, which overhangs the nostrils. The nasal bones attain maximum width anteriorly.

Teeth one pair, located on the anterior tip of the lower jaw, and projecting anterior to the upper jaw when the mouth is closed.

The sternum consists of five sections. Cervical vertebrae 7, thoracic 9-10, lumbar 10-11, and caudal 19-22; total 46-49. The anterior three or four cervical vertebrae are usually fused. Phalangeal formula: I_1 , II_{3-6} , III_{5-6} , IV_4 , and V_{1-2} . Ribs 9 pairs.

Biology not well studied. These animals represent forms of the open sea and feed apparently on mollusks. The periods of mating and parturition are prolonged.

These whales are distributed in the World Ocean but are few in number everywhere.

The genus consists of a single species: Cuvier's beaked whale, *Ziphius cavirostris* G. Cuvier, 1823.

There is no special hunting of these whales. (V.S.)

CUVIER'S BEAKED WHALE

Ziphius cavirostris G. Cuvier, 1823

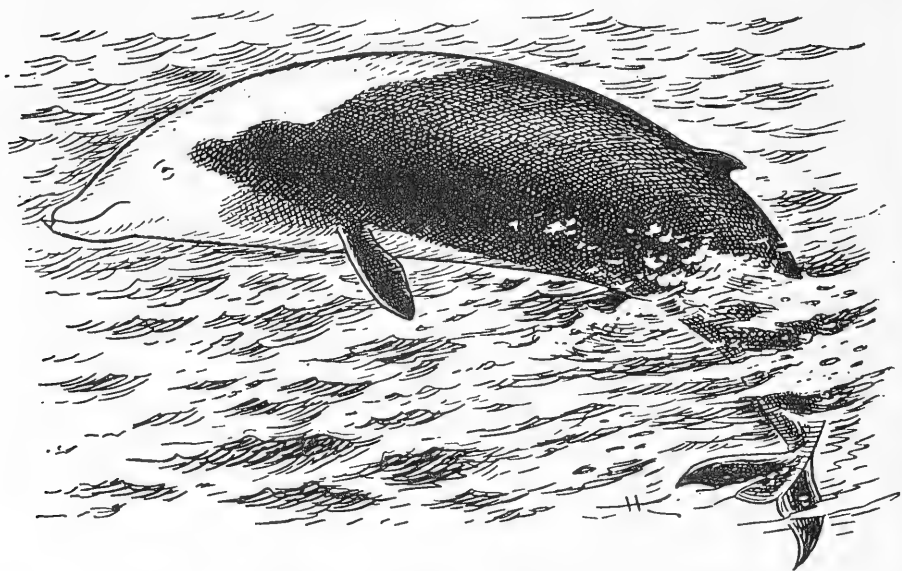
1823. *Ziphius cavirostris*. G. Cuvier. Rech. Oss. Foss. ed. 2, 5 (1), p. 350, pl. 27. French coast in the department of Rhone delta (Bouches-du-Rhone), Mediterranean Sea.
1826. *Delphinus desmaresti*. Risso. Hist. Nat. Eur. Mérid., 3, p. 23. Mediterranean Sea.
- 648 1883. *Ziphius grebnitzkii*. Stejneger. Proc. U. S. Nat. Mus., 6, p. 77. Commander Islands. (V.H.)

Diagnosis

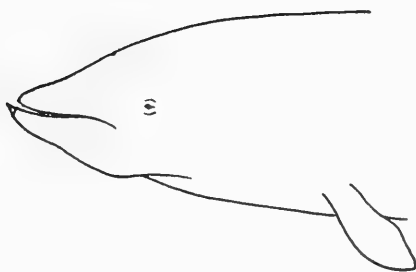
Only species of the genus.

Description

The frontal projection is much lower than in bottlenose whales and Pacific beaked whales (Figs. 381 and 382). The characteristic small oral cavity is smaller than in other species of the family of beaked whales. Two longitudinal grooves traverse the throat. The bulge of the crescent-shaped blowhole faces backward.



648 Fig. 381. Cuvier's beaked whale, *Ziphius cavirostris* (figure by N.N. Kondakov).



648 Fig. 382. Head of Cuvier's beaked whale, *Ziphius cavirostris* (figure by N.N. Kondakov).

The body color is subject to great individual variation. Monochromatic black, gray, or bluish-gray animals are encountered. In others, the ventral side may be lighter in color than the dorsal but the opposite, albeit less often, has also been recorded. Other color variations are likewise possible. Many depigmented patches of various shapes and sizes are seen on the skin. The head and dorsum (up to the dorsal fin) are sometimes very light-colored in old animals.

The rostrum of the sharply asymmetric skull is poorly set off from the cranium. Adult males are characterized by a mesorostral ossification that is more prominent than in females and the young. This ossification lies in a very deep longitudinal depression of the rostrum between the premaxillae.

649 The teeth of males are larger and more massive than in females (tooth diameter in males 25-29 mm, in females 10-14 mm). Young animals have 28-30 vestigial teeth in the gums of the upper and lower jaws. These teeth reduce in number as the animal ages. Cuvier's beaked whale has 7 cervical, 9 thoracic, 11 lumbar, and 20 caudal vertebrae. The proportions of these sections to the length of the entire vertebral column are respectively 3, 17, 36, and 44% (Slijper, 1936a). The stomach of Cuvier's beaked whale has five sections; the first and last are large and the three intermediate ones small; all of them are smooth-walled (Kenyon, 1961).

The main body measurements of three females and one male Cuvier's beaked whale (Tomilin, 1957; Kenyon, 1961) are respectively (in cm): body length 579, 584, 658, and 543; distance from tip of snout to posterior edge of dorsal fin 389, 391, 425, and 350, to the axillae 115, 142, 132, and 131, to the blowhole 60, —, 66, —; length of flippers 46, —, 56, and 42; maximum width of flippers 16, 17, 17, and —; height of dorsal fin 30, 19, 25, and 21; and width of caudal flukes from tip to tip 162, 182, 175, and 133. The largest of the animals caught had a body length of 793 cm.

Females are larger than males. Of 51 males and 34 females caught in Japan, the average length of the males was 550 cm (maximum 671 cm), of the females 580 (701) cm (Table 66).

The following are the basic skull measurements (Fig. 383) of two adult males and a female Cuvier's beaked whale (Tomilin, 1957) (in cm): condylobasal length 85, 81, and 88; zygomatic width 54, 52, and 53; length of rostrum 48, 46, and 47; width of rostrum at base 33, 32, and 48; length of left half of lower jaw 75, 74, and —; and length of mandibular symphysis 18, 16, and 18. (V.S.)

Geographic Distribution

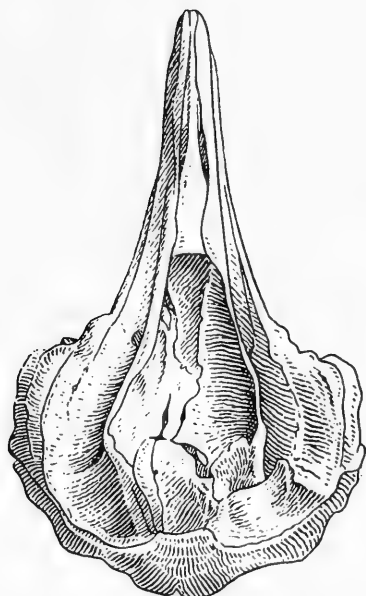
Warm, temperate, and partly temperate-cold waters of the World Ocean.

Geographic Range in the USSR

Constitutes a very small part of the entire range of the species. Cuvier's beaked whale has not been sighted with certitude in our waters of the basin of the Atlantic Ocean but may be encountered on our coasts of the Baltic Sea since it is known from Kattegat and waters of southern Sweden (transgressions): in the Far East, waters of southeastern Kamchatka and the Commander Islands where beached animals are a regular annual feature. According to less reliable information, the animal has been sighted near the Kuril Islands and off the southern coast of Sakhalin (Sleptsov, 1961).

649 Table 66. Dimensions of Cuvier's beaked whales caught in Japan (Omura, Fujino, and Kimura, 1955)

Body length, cm	Number of whales		
	Males	Females	Total
305	1	—	1
335	—	—	—
366	—	2	2
396	3	2	5
427	2	1	3
457	4	—	4
488	2	4	6
518	4	2	6
549	9	5	14
579	8	6	14
610	7	5	12
640	7	5	12
671	4	1	5
701	—	1	1



649 Fig. 383. Skull of Cuvier's beaked whale, *Ziphius cavirostris* (figure by N.N. Kondakov).

Geographic Range outside the USSR (Fig. 384)

Encountered in the North Atlantic Ocean along the coasts of the British Isles and southern Sweden, close to the coasts of Spain, Italy, France, and Corsica (Ligurian Sea), northern Africa, in the Mediterranean Sea, and in the Atlantic waters of North America. It is known in the Pacific Ocean around the Hawaiian Islands, in the East China Sea, along the coasts of Japan, and the Pacific Ocean coast of North America from California to the Pribilof Islands in the north. In the Southern hemisphere, it has been observed in the waters of Brazil, Argentina, South Africa, close to Sri Lanka, Polynesian Islands, around Australia, Tasmania, and New Zealand. Beached animals have been recorded at the following points: on the British Isles and Shetland Islands, in Kattegat Strait and on the coasts of Boguslan (Sweden), in the Baltic Sea, Bay of Biscay, Mediterranean Sea (near Nice, in the Rhone delta, at Malaga near Valencia, on Corsica, on the coast of Italy at Liguria, Messina Bay, and on the coast of Algeria), on the coast of North America in the states of New Jersey, Massachusetts, South Carolina, Rhode Island, California, and Alaska, and in British Columbia (Fig. 385). A large number of beached animals is known even in the Southern hemisphere (Tomilin, 1957; Clarke, 1958; Chapskii, 1963). Comparatively uncommon throughout its range. (V.A.)

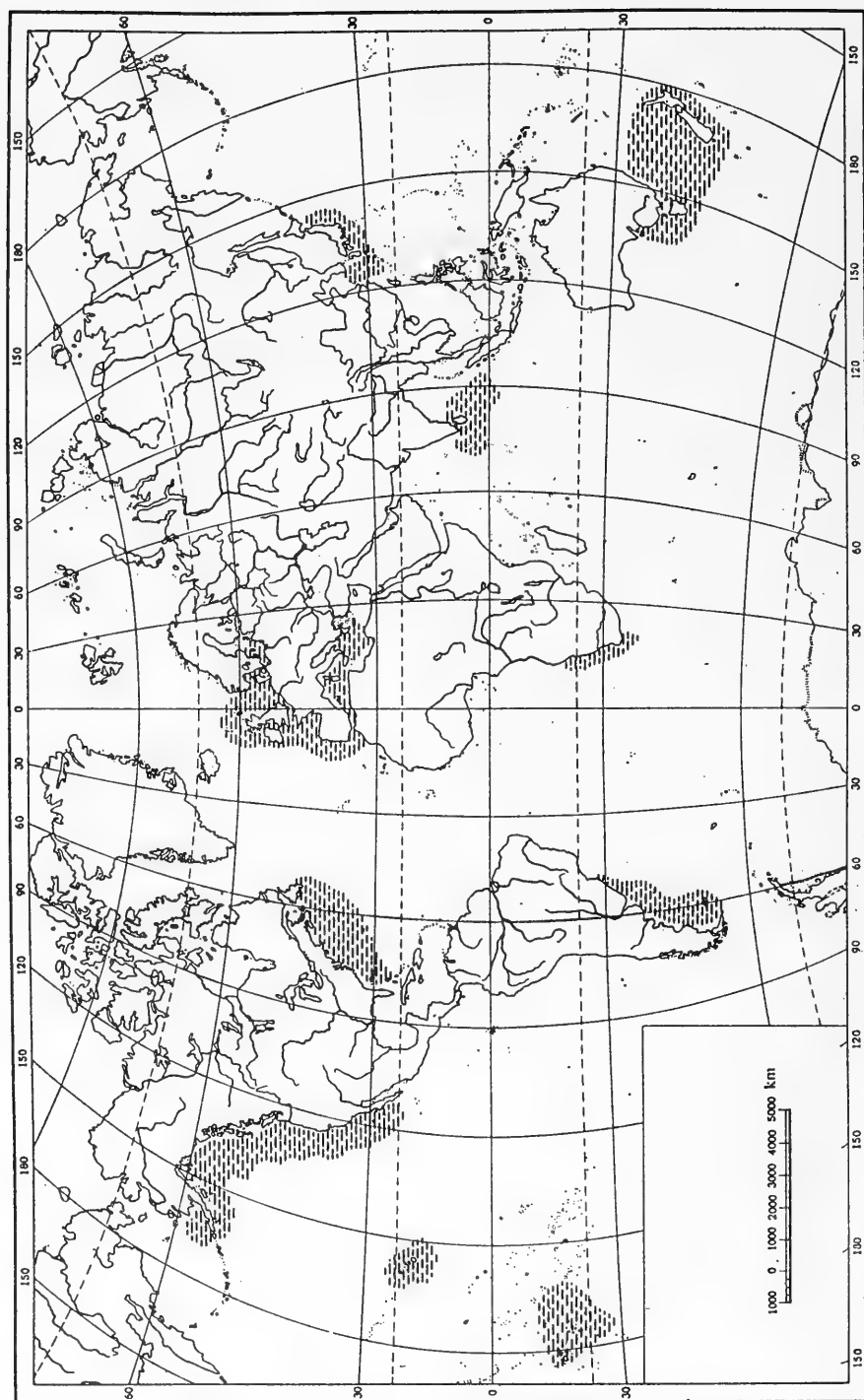
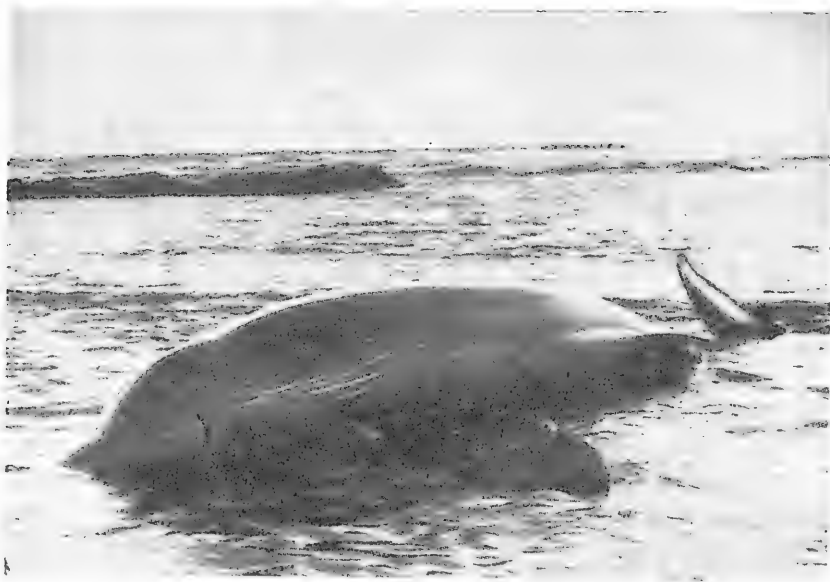


Fig. 384. Species range of Cuvier's beaked whale, *Ziphius cavirostris* (V.A. Arsen'ev).



651 Fig. 385. Above: Cuvier's beaked whale near Cape Chernyi, Mednyi Island, July, 1962. Below: Cuvier's beaked whale stranded on the shore of Bering Island, May, 1960 (photographs by S.V. Marakov).

Geographic Variation

Not studied.

Biology

Population. Comparatively common in our waters along the eastern coast of Kamchatka, especially around the Commander Islands; very rare or sighted occasionally elsewhere.

Food. Data on this aspect are negligible. It can only be assumed that cephalopods serve as the main food of Cuvier's beaked whale. Of the three stomachs dissected on the Commander Islands, one was empty and two contained the beaks of squids and crystalline lenses of cephalopods (Tomilin, 1957). The stomach of a female found on Amchitka Island (Aleutians) held the remains of 1,300 cephalopod mollusks—squids *Gonatus* sp.—in the form of beaks, lenses, etc. (Kenyon, 1961).

Behavior. These whales live in small groups, remain on the sea surface for about 10 min, dive together, and spend 10 to 30 min or more under water.

Seasonal migrations and transgressions. Along the Commander Islands (in the northern region of distribution), these animals are sighted in March and continue to be seen until autumn. Along the coasts of Japan, these whales are caught year-round although the best hunting season is from May through October, peaking in August. Hunting is carried out from coastal stations located exclusively on the Pacific Ocean coast of Honshu and on the northeastern coast of Hokkaido. In the Sea of Okhotsk and along the coast of the Sea of Japan, where Baird's beaked whales are hunted, Cuvier's beaked whales are not caught (Omura, Fujino, and Kimura, 1955). Apparently Cuvier's beaked whales are also encountered along the coast of California almost year-round, as supported by the following records of whales stranded at roughly 41° N lat.: a large female on February 17, 1963; an adult female on September 22, 1959; an adult male on March 2, 1957; and an immature small male on November 24, 1957 (Mitchell and Houck, 1967).

653 *Reproduction, growth, and development.* The periods of mating and parturition have not been established but in all probability both are protracted. In 1951, 1952, and 1953, embryos 30, 97, and 213 cm long were detected in August; embryos 170 cm long in September; and others 43 cm long in October, 1952 (Omura, Fujino, and Kimura, 1955). An embryo 267 cm long, found in a dead female on Bering Island (Commander Islands), was fully developed (Tomilin, 1957). Probably the size of newborn Cuvier's beaked whales is proximate to the above range. Males attain sexual maturity at a body length of 5.5 to 5.9 m; their testes weigh

3.5 to 4.2 kg; females become mature at a body length of about 5.5 m. A female 658 cm long, cast on Amchitka Island (Aleutians), contained at least two traces of corpora lutea of pregnancy. This female had 24-28 layers in her tooth dentine and thus her age was estimated at 12-14 years. A male with a body length of 544 cm, found on the same island, had 13 layers in the tooth dentine or was six-seven years of age (Kenyon, 1961).

Enemies, diseases, parasites, mortality, and competitors. Two species of nematodes and one of cestodes are known in Cuvier's beaked whale. The nematode *Crassicauda crassicauda* Creplin parasitizes, in addition to Cuvier's beaked whale, the urogenital system of another species of toothed whales and six species of baleen whales; *Crassicauda boopis* Baylis, parasitizing the urogenital system of Cuvier's beaked whale, the humpback whale, and the fin whale, was found in the Atlantic Ocean in the Northern and Southern hemispheres. A cestode, *Phyllobothrium* sp., was detected in the blubber of Cuvier's beaked whale (Delamure, 1955; Tomilin, 1962).

Field characteristics. The body length of adult whales averages 5-7 m. The "beak" is broad and short and the forehead low and sloped. The blowhole is crescent-shaped and its horns turned anteriorly. Teeth one pair, located in the anteriormost part of the lower jaw, and not concealed by the upper jaw, projecting anterior to its edge when the mouth is closed. These animals live in small groups. While diving, the group disappears under water in unison. (V.A.).

Economic Importance

Only a few tens of Cuvier's beaked whales are caught annually and as such this species has no economic importance whatsoever. It is caught along with other species of small whales from the coastal stations along the Pacific Ocean coast of Japan. From 1948 through 1955, 3, 10, 27, 35, 36, and 40 animals were caught annually (Omura, Fujino, and Kimura, 1955).

Sexually mature males ranging from 5.5 to 6.5 m in length constituted the major part of the catch.

Weight of the Body Parts of Male Cuvier's Beaked Whale, Body Length 658 cm (kg) (Kenyon, 1961)

Flesh, blubber, bones (including head)	2,717.0
Heart	15.4
Lungs	39.4
Liver	25.9
Kidneys	16.4

Reproductive organs	20.7
Stomach:	
Empty	17.7
Its contents	18.6
Intestine with contents	41.3
Spleen	0.1
Aorta, bronchi, and connective tissue	31.6
Blood (some inevitably lost)	8.1
Total	<hr/> 2,933.7 <hr/>

654 Hunting is carried out mainly from small boats and using small-bore harpoon guns. A good number of animals fall into nets. The products are used like those of other small whales. On the Commander Islands the flesh and blubber of beached Cuvier's beaked whales are fed to dogs and foxes.

There is no hunting of this whale in our range. (V.A.)

Genus of Bottlenose Whales

Genus *Hyperoodon* Lacépède, 1804

1804. *Hyperoodon*. Lacépède. Hist. Nat. des Cétacées, pp. XLIV, 319.

Hyperoodon butskops Lacépède = *Balaena ampullata* Forster.

1804. *Anarnak*. Lacépède. Ibid., pp. XXVIII, 164. *Anarnak groenlandicus*

Lacépède = *Balaena ampullata* Forster. (V.H.)

Medium-size whales.

The "beak" is prominently displayed, more sharply than among other species of the family. The frontal projection of the prominent corpus adiposum [forehead] descends rather steeply from the base of the beak. The corpus adiposum is better developed in males than in females. Two to four longitudinal grooves occur on the throat. The dorsal fin is flexed along the posterior edge.

The body is blackish-gray but light gray or yellowish-gray on the abdomen.

In the skull the maxillae dorsally form at the base of the rostrum two (right and left) lateral crests which are particularly well developed in adult males. The rostrum is long. The nasal bones are large and concave at the top and the mesethmoid bone is incompletely ossified. Together with the premaxillae, the former bones rise posterior to the bony nares vertically upward and even overhang them. The maxillae have high crests that extend along the edges of the rostrum. One pair, less often two pairs of teeth develop at the tip of the lower jaw. The teeth are larger in males

than in females. Cervical vertebrae 7, thoracic 9 (8), lumbar 9-11, and caudal 18-20; total 43-46. The cervical vertebrae are fused. The sternum consists of three sections. Phalangeal formula: I_{1-2} , II_{5-6} , III_5 , IV_{4-5} , and V_{2-3} .

These animals feed mainly on cephalopods. The periods of mating and parturition are prolonged. The duration of gestation is about a year.

They are distributed in the North and South Atlantic Ocean, and in the Indian and Pacific oceans. Seasonal migrations take place.

The genus comprises two species: northern bottlenose whale, *Hyperoodon ampullatus* Forster, 1770, and southern flat-faced bottlenose whale, *Hyperoodon planifrons* Flower, 1882.

Mesoplodon planifrons [*Mesoplodon pacificus*], described by Longman in 1926, is sometimes treated as a synonym of *Hyperoodon planifrons* (Hershkovitz, 1966), or as a subspecies of *Mesoplodon mirus* Moore, 1960 (Moore, 1960), or as a lone species of a different genus, *Indopacetus* Moore, 1968 (Moore, 1968). Additional data are required before an accurate conclusion can be drawn (descriptions are based on just two skulls).

Only the northern bottlenose whale is encountered in the seas of the USSR. There is no special hunting of this species in our waters. (V.S.)

NORTHERN BOTTLENOSE WHALE

Hyperoodon ampullatus Forster, 1770

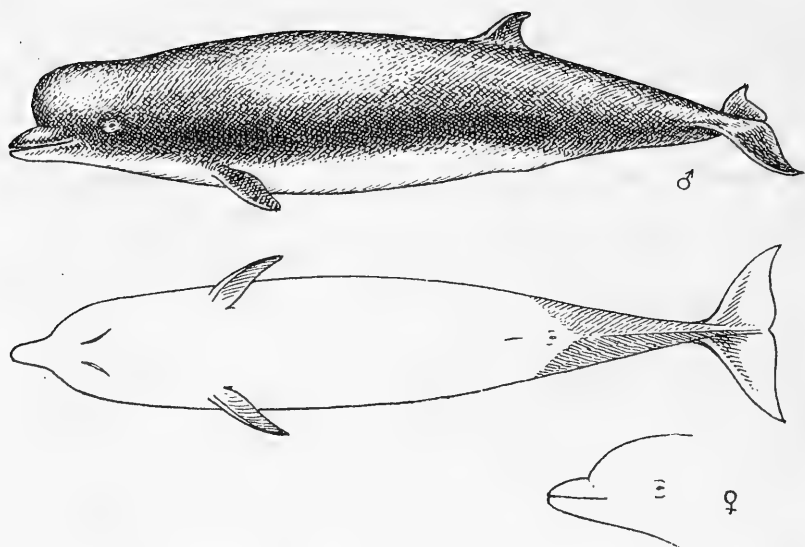
1770. *Balaena ampullata*. Forster. Kalm's Travel into N. America, I, p. 18. Maldon, Essex, England.
1776. *Balaena rostrata*. Müller. Zool. Danicae. Prodr., p. 7. Waters of Denmark and Norway.
1789. *Delphinus butskopf*. Bonnaterre. Tabl. Encycl. Méth. des Trois Regnes de la Nature. Cétologie, p. 25. Honfleur, France.
- 655 1822. *Delphinus hyperoodon*. Desmarest. Encycl. Méth. Mamm., 2, p. 520. Thames, England. (V.H.)

Diagnosis

Only species of the genus found in waters of the USSR.

Description

Dorsal fin with a concave posterior margin and located above the anal opening (Fig. 386). The flippers are larger in males than in females. The bulge of the crescent-shaped blowhole faces the tail. Two (sometimes



655 Fig. 386. Northern bottlenose whale, *Hyperoodon ampullatus* (figure by N.N. Kondakov).

four) longitudinal grooves extend along the throat. Four hairs are seen on each side of the snout in the embryo.

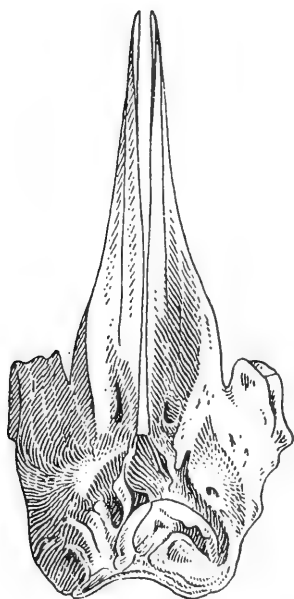
The body is blackish-gray dorsally and light gray ventrally. The fins are grayish-black. With advancing age, the color turns light, almost yellow. The skin is covered with numerous white spots, apparently caused by a fungal disease.

Two pairs of teeth are seen only in some adult animals. In females and many males the posterior pair of teeth does not emerge or, if it does, these teeth are notably smaller than the anterior pair, which may reach a height of 6.5 cm. The anterior teeth are set at the tip of the lower jaw and project outside when the mouth is closed. The second pair of teeth (when present) is separated from the first pair by a considerable gap.

Males are larger than females. The largest of the measured males was 9.4 m in length, of females 8.7 m.

656 Measurements (as percent of animal length) of a young male with a body length of 518 cm and an adult female 716 cm long (Tomilin, 1962) are respectively: from tip of snout to commencement of dorsal fin 52.9 and 57.4; height of dorsal fin 5 and 5.3, length of dorsal fin 7.8 and 8.5; spread of caudal flukes between tips 27.1 and 29.1; length of flippers 10.7 and 8.5, and width of flippers 5.3 (female).

The skull dimensions are (Tomilin, 1957) (in cm): condylobasal length of skull 145 (100%), zygomatic width 68 (46.9%), length of



655 Fig. 387. Skull of the northern bottlenose whale, *Hyperoodon ampullatus* (figure by N.N. Kondakov).

rostrum 89 (61.4%), width of rostrum at base 35 (21.4%), length of lower jaw 135 (93.1%), and length of mandibular symphysis 25 (17.2%). (V.S.)

Geographic Distribution

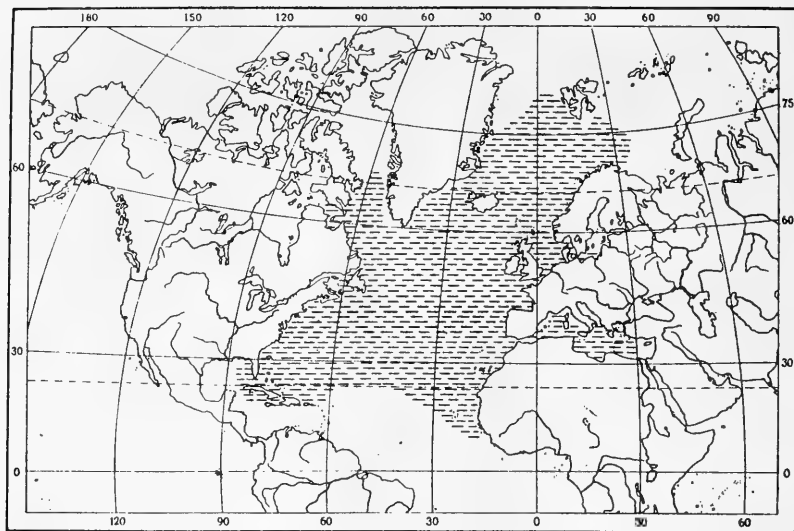
North Atlantic Ocean, usually at depths exceeding 1,000 meters (Jons-gard, 1952).

Geographic Range in the USSR

Rare in our waters but sometimes encountered in the central part of the Barents Sea, along the Murman coast, and less often along the western coasts of Novaya Zemlya. Transgresses occasionally into the White Sea where instances of some animals being caught are known. Transgressions have also been observed in the southern part of the Baltic Sea (in winter).

Geographic Range outside the USSR (Fig. 388)

In the eastern part of the North Atlantic, these animals inhabit waters from the Cape Verde Islands in the south (15 to 18° N lat.),



656 Fig. 388. Species range of the northern bottlenose whale, *Hyperoodon ampullatus* (V.A. Arsen'ev).

along the entire European coast, and up to the Arctic. They cover the Mediterranean Sea, are encountered along the coasts of Holland, Great Britain, Shetland and Faroe Islands, and coasts of Norway up to Varangerfjord. They inhabit the waters of Iceland and Jan Mayen Island, are common in the Norwegian and North seas, and penetrate the waters of Spitsbergen in the zone of influence of the Gulf Stream (75-78° N
657 lat.) toward the coast of Greenland. They transgress into the southern part of the Baltic Sea (Kiel and Lübeck bays, Rügen Island) but are rare on the Baltic coasts of Sweden and Norway. Known in the west from Rhode Island in the south up along the coast of North America (New York and Massachusetts bays) to Newfoundland, Hudson, Davis, etc. (Tomilin, 1957, 1962¹⁰; Chapskii, 1963). (V.A.)

Geographic Variation

Not established.

¹⁰ References to the existence of this bottlenose whale in the Pacific Ocean, extensively cited in the literature, including the latest reviews (see, in particular, Hershkovitz, 1966: "Bering Sea and Japan"), are erroneous and pertain to Baird's beaked whale (*Berardius bairdi*; Tomilin, 1952, 1957; see latter). (V. H.)

Biology

Population. The population of the northern bottlenose whale, compared with that of large whales, is very small. Hunting has never exceeded 500 bottlenose whales per year.

Food. Cephalopods (*Gonatus fabricii*, *Onychoteuthis* sp., *Sepia* sp., and *Loligo* sp.) constitute the main food. Most of the stomachs investigated revealed only the beaks of cephalopods, which numbered up to 10,000 in one stomach. Herring, cod, sea-cucumbers, and starfish were found as random food objects. The characteristic structure of the teeth and the ability of the northern bottlenose whale to dive to great depths confirm the view that these whales specialize in feeding on cephalopods (Tomilin, 1957).

Daily activity and behavior. This whale is usually encountered in small groups, sometimes up to 20 animals. Single animals are rare. Groups most often comprise animals of different sexes and ages, including calves. Such groups resemble the harems of sperm whales since usually a single large male is seen in them. However, groups consisting exclusively of adult males have also been observed. At places of food concentration, groups of bottlenose whales sometimes gather into large herds of up to a hundred or more animals.

Like the sperm whale, the northern bottlenose whale possesses the ability to descend to great depths and remain submerged for a long while. It has been suggested that the duration of its underwater residence may be as much as one hour. Herein lies some similarity of behavior during diving with the sperm whale. On surfacing after prolonged submergence, the northern bottlenose whale inhales/exhales quite a number of times and remains on the surface for a long time. It then undertakes another long dive. While resting, up to thirty brief intermediate submergences, one every 30-40 sec, producing small (50-60 cm high), barely perceptible blows have been recorded for this whale. A display of the caudal flukes during diving has never been seen. The auditory faculty is thought to be very well developed in the northern bottlenose whale and it is sensitive to extraneous noises. The herd instinct is strong in these animals and they do not usually abandon an injured mate even when confronted with imminent danger themselves.

Seasonal migrations and transgressions. The northern bottlenose whale performs regular seasonal migrations but the courses and periods of its spring and autumn migrations have hardly been studied. It is only known that these whales inhabit the northern part of their range in the summer months and enter the southern part in winter. Spring migrations commence early since they are noticed off the coasts of Norway and

658 even Jan Mayen in March and April. The line of sharp increase in depth represents the boundary of distribution of these whales and they usually transgress no farther. Thus they never enter the fjords. Only one case is known; a small herd of bottlenose whales appeared in Oslo Fjord in September, 1939 and one whale beached (Jonsgard, 1952*). In June these whales are sighted along ice edges up to 77° N lat. and have even been encountered (sometimes in large numbers) among drifting ice. Off the coasts of Norway and in other regions of their hunting, the maximum number of bottlenose whales is caught in May and a slightly smaller number in June Østby, 1956, 1957, 1958, 1959). It has been assumed that this species penetrates farthest north in spring and later descends slightly southward to inhabit the waters of the Falkland and Shetland islands and east of Iceland. Most of the northern bottlenose whales are confined to the region where the Gulf Stream waters mix with Arctic currents, i.e., the most productive regions. They transgress only into those cold waters which fall under the influence of the Gulf Stream. Autumn migrations have not been traced; the whales depart from the northern regions commencing probably September and extending up to late autumn. Wintering sites have not been established; it would appear that they overwinter in the southern part of their range.

Many instances of beached bottlenose whales are known on the coasts of France, the FRG, the GDR, Holland, Denmark, Sweden, Norway, England, Ireland, Scotland, Faroe and Lofoten islands, and Iceland. Beaching has also been recorded on the American coast in Rhode Island and Massachusetts states and in New York bay and the Gulf of St. Lawrence. Beached bottlenose whales have even been found on the coasts of Greenland and Spitsbergen.

Finds of bottlenose whales in the White and Baltic seas can be regarded as transgressions (Tomilin, 1957, 1962).

Reproduction. The period of mating has not been established; gestation extends for 12 and probably even for 15 months. Births occur in the spring, evidently in March-April or in April-May. The sites of mating and parturition have not been identified.

Growth and development. Data on these aspects are extremely fragmentary and few. The largest of the embryos studied was 305 and even 350 cm long. Apparently the newborn calf ranges from 200 to 250 cm in length, although the smallest of those measured was only 183 cm long. During lactation the calves double in length (duration of lactation is presumably five to seven months). The length of calves fed on milk varied from 244 to 488 cm. By the third year these whales attain a length of 6 m (Tomilin, 1957). Females become sexually mature at a body length

of 7 m. The smallest (of measured) pregnant females was 6.4 m long (Jonsgard, 1952*).

Enemies, diseases, parasites, mortality, and competitors. The killer whale is regarded as an enemy of bottlenose whales but there are no direct observations of killer whale attacks on them. Diseases have not been studied; some cases of bone tumors have been recorded in museum skeletons.

The whale louse *Platycyamus thompsoni* Gosse, mainly infesting the head, "beak," and mouth corners, is a known ectoparasite of the northern bottlenose whale. Among the barnacles, *Conchoderma cuvieri* is more commonly encountered and *C. auritum* rarely, in the teeth and light-colored sections of the skin. *Penella crassicornis* penetrates the skin.

Seven species of helminths have been registered. The cestode *Strobilicephalus triangularis* Diesing, parasitizing the intestines, has been found in the northern bottlenose whale and three species of baleen whales from the waters of Portugal and Brazil; *Diphyllbothrium delphini* Bosk (larvae) has been detected in the adipose depots of these same whale species. The nematode *Anisakis simplex* Rudolphi, localizing in the gullet, stomach, and intestines of the northern bottlenose whale, is very widely distributed among marine mammals. It has been found in many species of baleen and toothed whales and, among pinnipeds, in Steller's sea lion caught in the North Sea, off the coasts of Kamchatka, and in the waters of Japan and New Zealand. Another nematode, *Crassicauda benneti* Spaul, has been cited for "bottlenose whale" without mention of the species. Of the two species of acanthocephalans, *Bolbosoma turbinella* Diesing parasitizes in addition to the northern bottlenose whale, the intestine of six species of baleen whales from the waters of Iceland and Australia. Finally, *Bolbosoma turbinella* [sic.] Diesing, found in the intestine of the northern bottlenose whale, has been detected in five species of baleen whales.

The mortality of bottlenose whales has not been established (Delamure, 1955; Tomilin, 1957).

Field characteristics. Long, beak-shaped snout, steeply dropping high forehead, and the white color of old males are prominent features. One pair of teeth on the anterior tip of the lower jaw projects outward when the mouth is closed (sometimes a second pair projects slightly among very old males). The upper side of the body of young animals is black or grayish-black and of old animals light brown. When diving deep, this species flexes the body strongly but never displays the caudal flukes. Between two prolonged submergences, it remains for a long time on the water surface, producing 20-30 blows during this period. The blow

is low, bushy, 50-60 cm high, and barely perceptible. The respiratory sound is short and interrupted with a metallic timbre. (V.A.)

Economic Importance

Commencing from the 1880s, regular hunting of the northern bottlenose whale was practiced in Norway but the output was low. Hunting intensified due to a drop in catch of right whales and several hundreds of bottlenose whales were caught in some years. However, by the beginning of the twentieth century, as a result of the rapid development of the hunting of large fin whales and reduction in the population of bottlenose whales, the catch of the latter decreased sharply. Hunting was initially carried out predominantly along the coasts of Greenland but later most of the whales were caught in Norwegian waters (Table 67).

Commencing in 1929, modern specialized hunting of small whales (including the bottlenose whale) employed small motor boats equipped with small-caliber (50-60 mm) harpoon guns. Among the small whales caught, the Minke whale occupied first place followed by the bottlenose whale. In the 1930s, this hunting, especially of the Minke whale, was of great economic importance to the Norwegian fishermen.

The maximum number of bottlenose whales was caught in the water body between Jan Mayen, Iceland, and Faroe Islands, and later west of Medvezhii Island and Spitsbergen and in the deepwater regions off the Norwegian coast.

Table 67. Catch of northern bottlenose whales in Norway (international whaling statistics)

Year	Catch of whales	Year	Catch of whales
1938	70	1954	70
1939	45	1955	124
1940	8	1956	267
1941	21	1957	163
1942	9	1958	145
1943	34	1959	94
1944	40	1960	193
1945	22	1961	87
1946	22	1962	321
1947	108	1963	267
1948	59	1964	307
1949	220	1965	692
1950	48	1966	340
1951	77	1967	264
1952	17	1968	384
1953	49		

660 A single northern bottlenose whale yields about a ton of fat, on average (large animals up to two tons), in addition to 200 kg of spermaceti. The fat is used only for commercial purposes. The spermaceti of the bottlenose whale is similar to that of the sperm whale in chemical composition. The hollow of the lower jaw of the bottlenose whale contains a small amount of oil with a typical chemical composition; it does not congeal in the cold and can be used for lubricating fine mechanisms. The raw meat causes disorders of the digestive tract but this adverse phenomenon disappears with cooking and the meat is suitable for feeding dogs and fur-bearing animals. It is not used for human consumption. This whale is not hunted in the Soviet Union. (V.A.)

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MAMMALS OF THE SOVIET UNION

Volume I

V.G. HEPTNER, A.A. NASIMOVICH, A.G. BANNIKOV

This volume of *Mammals of the Soviet Union* is devoted to a description of artiodactyls and perissodactyls found in the Soviet Union. These animals are of great scientific and economic interest; information on them, especially in recent Soviet literature, is voluminous. In recent years world literature on this subject has likewise been considerably enriched with new data. The abundance of information on ungulates explains the size of the present volume. All the characteristics of groups have been described according to a common scheme; deviations occur in a few cases, however. These characteristics are stated briefly and pertain to the group as a whole; they are not exclusive to species of the Soviet fauna. All species are described according to a common plan, altered only in the case of some extinct forms. In devising the scheme for descriptions of species not only the convenience of the reader was kept in mind, but the hope that gaps in our knowledge would become self-evident and stimulate further research.

MAMMALS OF THE SOVIET UNION

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